RESEARCH THESIS

PH.D

UNIVERSITY OF THE WITWATERSRAND

Competition vs facilitation: species interactions within the short grass grazing guild

Researcher: Randal rsenault.....Date.....

Centre for African Ecology (CAE)

Department of Zoology

University of the Witwatersrand

Supervisor: Prof. N. Owen-Smith …….....Date.....

Centre for African Ecology (CAE)

Department of Zoology

University of the Witwatersrand

Contents

Acknowledgements……3
Abstract.....3

CHAPTER ONE
Introduction…….....5
Aim…….....12
Objectives……..…….....12
Questions Addressed……12
Thesis Outline……..13

CHAPTER TWO
Facilitation versus competition in grazing herbivore assemblages……..20
- published in Oikos 97: 313-318 (2002).

CHAPTER THREE
Resource Partitioning by grass height among grazing ungulates does not follow body size relation……36

CHAPTER FOUR
Competition versus Facilitation: the comparative use of grass resources by short grass grazers……55

CHAPTER FIVE
The effect of white rhino grazing on grazing lawns in Hluhluwe-iMfolozi Park, South Africa……..……98

CHAPTER SIX
Conclusions……..……...……...…..110

ACKNOLEDGEMENTS

A big thanks to all the people who have helped in this research. Special thanks to Norman Owen-Smith and NRF, Neville Pillay, and all the office staff at Wits University; thanks to all at Hluhluwe-Imfolozi Park, including Dave Balfour, Paul Harveman and Thobile; thanks to my Nissan Bakkie for getting me around and only losing one engine; thanks to all the animals for not eating me or running me down; thanks to all my friends in Jo'burg and Cuckoo's Nest for the constant diversions; thanks to music for exercising my left brain; and finally thanks to Mom, Dad and Nan for your continual love and support. A Ph.D is a stimulating hobby!

ABTRACT

How so many species coexist while utilizing the same resources is both of ecological interest and important for the management of wildlife communities and parks. This thesis endeavours to understand how grazing herbivores co-exist, with special emphasis on understanding the mechanisms of competition and facilitation over temporal and spatial scales. I compared the dry season use of grasslands, grass species, grass height and grass greenness by white rhino and three other ungulate species, zebra, wildebeest, and impala. I was specifically interested in the extent to which white rhinos, with their capacity to graze both short and tall grass, either competed with or facilitated other grazers.

In Chapter Two, I clarify the mechanisms of facilitation and competition in terms of temporal and spatial scales, and discuss why there is little evidence in the literature to support these mechanisms. I conclude that evidence for facilitation through stimulation of grass re-growth during the growing season appears stronger than that for increased resource access through removal of obstructing grass structures during the dormant season. Facilitation may benefit the nutritional gains obtained by certain species in the short term, but these benefits do not appear to be translated into the expected population consequences. In collaboration with co-author Norman Owen-Smith, we suggested this

could be due to seasonal tradeoffs between facilitation and competition, as well as to restrictions on the spatial extent of trophic overlap.

In Chapter 3 Norman Owen-Smith and I compared the grass height use in relation to body size. We expected that the grass height favoured would increase with the body size of the herbivore species, as suggested from past studies of resource partitioning among large mammalian herbivores. Instead we found that the largest of these species, white rhino, concentrated on the shortest grass, while the smallest species, impala, favoured grass heights intermediate between those grazed by wildebeest and zebra. Results suggest that the scaling of mouth width relative to body size, and hence metabolic demands, is the primary factor governing grass height selection, rather than body size alone. Hence grazing successions governed by body size differences may not be a typical feature of their ecology, contrary to past suggestions. Furthermore, there was considerable overlap in grass height grazed among these four species, indicating that niche separation by grass height is inadequate alone to explain their coexistence. More attention needs to be paid to other aspects such as the grass species selected and habitat structure favoured.

Chapter Four compared the overlap in grassland use and grass species use, as well as grass height and grass greenness of swards utilized by the herbivores as the dry season advances. I show that all species prefer grazing lawns during times of abundance, and that zebra leave grazing lawns before other species, and wildebeest leave grazing lawns before white rhino and impala. This suggests zebra and wildebeest may be competitively excluded from grazing lawns through a reduction in grass height, by white rhino and impala, during the dry season. However, white rhino are also potentially the ‘supreme’ facilitator increasing the availability of nutritious grazing lawns, as well as increasing the quality of those lawns through grazing in the wet season. A better understanding of the trade-off between “habitat facilitation” and competitive exclusion by white rhino, allows us to better understand how grazing herbivores co-exist.

CHAPTER ONE

INTRODUCTION

The diversity and abundance of ungulates in Africa is greater than anywhere else on earth. How so many species coexist while utilizing the same resources is both of ecological interest and important for the management of wildlife communities and parks. The above question can be asked differently as well, for example, why are there not more species present and what factors promote coexistence versus competitive exclusion of species within a community?

Interspecific competition has traditionally been considered the major factor governing the diversity of communities (Gause 1934; MacArthur 1972). Other factors which have been shown to be important, especially for large herbivores, are: a) facilitation (Vesey-Fitzgerald 1960; Bell 1970; Bell 1971; McNaughton 1976), b) predation (Sinclair 1985); c) migration (Fryxell et al. 1988; Fryxell and Sinclair 1988; Fryxell 1991; Murray and Illius 1996); d) spatial and temporal heterogeneity (Senft et al. 1987; Bailey et al. 1996; O'Reagain and Schwartz 1995); e) partitioning of resources in terms of body size and metabolism, feeding adaptations, and foraging behaviour (Schoener 1974; Schoener 1983; Schoener 1986; du Toit and Owen-Smith 1989; Owen-Smith 1989; Owen-Smith and Cummings 1993; Prins and Olff 1996).

My research was concerned with the utilization of food resources by the grazing ungulate guild at Hluhluwe-iMfolozi Park (HiP), and the interaction with grassland dynamics. Specifically, issues of facilitation and interspecific resource competition are addressed. The major species of the grazing herbivore guild of the Hluhluwe-iMfolozi Park (HUP) are white rhino, impala, wildebeest and zebra, which exist at high densities, approximately 32.7 kg/ha, 16.3 kg/ha, 8.9 kg/ha and 9.4 kg/ha, respectively.

White rhino, with an average mass of 1350 kg, have the potential for altering vast areas of grazing resources (Owen-Smith 1988). This may be detrimental or beneficial for wildebeest, zebra and impala through a reduction in grass abundance, or through the creation and maintenance of grazing lawns. White rhino grazing may affect the medium

sized ruminant, wildebeest and non-ruminant zebra, differently, due to their differences in feeding morphology and digestive strategy. In addition, the smallest species, impala, at their present density, may have the ability to reduce the height of short swards in the dry season, as well as the quality of grass swards, through increased selectivity for green grass.

Of the few studies that have looked at the interactions of African grazing ungulate species, most have taken place in the Serengeti, where the major grazing species is migratory wildebeest and megaherbivores are conspicuously absent. HiP is a closed park system where migration is not possible, it has a high density of grazers, a prolonged dry season, and the major grass consumer is the megaherbivore white rhino. HiP presents an ideal environment to address questions regarding facilitation and competition in relation to feeding morphology, body size, digestive strategy and seasonal changes in resource quality and quantity.

Facilitation and Grassland Dynamics

Facilitation is when the resource use of one species somehow benefits other species (Caughley and Sinclair 1994). Whether the benefit to species is in terms of individual resource use or population success is not well differentiated or documented. Studies have shown that the grazing by one herbivore species, for example wildebeest in the Serengeti, can increase the availability and quality of grass resources for other grazing species, such as Thomson's gazelle (McNaughton 1976; McNaughton 1979; McNaughton 1984), but whether this translates into population increases is not well understood. For the purposes of this discussion, it is beneficial to differentiate between feeding facilitation and population facilitation. Most studies, likely due to logistic constraints and the life span of ungulates, have focused on feeding facilitation and only suggest that this may be beneficial to populations.

Feeding facilitation or the facilitation of resource gains may occur in a number of different ways and over different time scales. For example, Vesey-Fitzgerald (1960) suggested that the browsing and trampling by elephants, on extensive reed beds around Lake Rukwa, Tanzania, benefited some grazing species by creating openings for lush

regenerating vegetation. Similarly, facilitation may occur when one herbivore species, such as white rhino, heavily graze tall grass stands, enabling shorter and more productive grass species to become established, benefiting other short grass grazers (Owen-Smith 1988).

As well as promoting the transformation of tall grasslands into short grass grasslands, which may be due to grazing pressure at any time of the year, feeding facilitation may occur through the maintenance of short grass areas through continual grazing pressure in the wet season. For example, herbivore grazing by one species may benefit other grazers by reducing the grass height of tall grasslands, as well as maintaining short grass grasslands already present.

McNaughton (1984) used the term 'grazing lawn' to describe the short grass patches where grass is kept in a high quality and a highly productive state through grazing. He found that above ground productivity was strongly influenced by grazing in the wet season. Moderate grazing stimulated productivity up to twice the levels of ungrazed plots, and productivity was maintained at control values even under very intense grazing in the wet season and continued longer into the dry season (McNaughton 1985).

Another form of feeding facilitation benefiting grazing herbivores is grazing successions. Facilitation through grazing successions were first suggested by Vesey-Fitzgerald (1960) and documented by Bell (1970; 1971). Vesey-Fitzgerald observed a grazing succession in southern Tanzania where the trampling and feeding of elephants created openings for vegetation which provided habitat for buffalo. The grazing of buffalo in turn promoted short grass which was used by antelope, such as topi (Vesey-Fitzgerald 1960).

A similar grazing succession of buffalo, zebra, wildebeest, topi and Thomson's gazelle, which mainly occurred in the dry season, was described in the Serengeti by Bell (1970; 1971). Bell looked at resource use of ungulates in areas of short, medium and tall grass occurring at different levels of the catena. In the wet season when all areas were green, all species were found on the top of the ridges where high quality short grass prevailed. Due to the high productivity of the grass, herbivores had little difficulty grazing grass leaves and gaining sufficient nutrients.

In the dry season, the growth of grass declined and short grass areas became progressively depleted. These changes affected the larger and non-ruminant species, buffalo and zebra, first, and then later affected the smaller and wider mouthed species, topi, wildebeest and Thomson's gazelle. Buffalo and zebra left the short grass areas first, to feed on medium and tall stands lower down the catena. By removing the tough stems on the medium and taller stands, buffalo and zebra made the grass leaves available for wildebeest and topi, which followed later in succession. The grazing of wildebeest and topi then enabled the smallest species, Thomson's gazelle, access to the lower levels of the herb layer (Bell 1970; Bell 1971).

Both Vesey-Fitzgerald and Bell suggest that the presence of species earlier in the succession, not only benefit other species through short term enhancement of grazing resources, but may also translate into increased population success for species later in the succession. Bell (1971), for example, stated that a decline in the population of zebra in the Serengeti, may lead to a decline in wildebeest.

It should be noted that although these classical examples of facilitation through grazing successions are widely referred to in the literature and are largely unquestioned, the assumption that the feeding of one species benefits from the grazing of other species earlier in a succession is based on correlative data (de Boer and Prins 1990; Putman 1996). For example, Bell's research was mainly based on the diet analysis of rumen and faecal samples (Gwynne and Bell 1968; Bell 1970). Further, any population benefits to species within the grazing succession have not been demonstrated.

Although short term resource gains may occur through feeding facilitation, this is not sufficient to prove a benefit to the population. This has been most clearly demonstrated by McNaughton (1976), and long term population censuses in the Serengeti (Dublin 1990). Using exclosure experiments, McNaughton (1976) clearly demonstrated that the grazing of the large migratory herd of wildebeest on grazing lawns stimulated young green re-growth which was preferred by Thomson's gazelle. Although the grazing of wildebeest was shown to facilitate the grazing of Thomson's gazelle in the short term, a large increase in wildebeest did not translate into an increase in the gazelle population (Sinclair and Norton-Griffiths 1982; Dublin et al. 1990).

The only clear example in ungulates of both feeding and population facilitation has been demonstrated for two species on the Isle of Rhum, Scotland. Gordon (1988) compared the effects of grazing by cattle on the populations and grazing of red deer. He found that a greater biomass of green grass was available to red deer in spring, in areas grazed by cattle during the winter, and that red deer preferred to graze in these areas. Also, red deer had more calves per female in areas previously grazed by cattle, compared to ungrazed areas (Gordon 1988).

Competition

Interspecific resource competition is when the resource use of one species reduces the availability or quality of resources to be used by another species (Tilman 1982). Within the herbivore grazing guild, the mechanism of competition is mainly exploitative through the depletion of grass resources during limiting seasons (Owen-Smith 2002).

In terms of grazing herbivores, the questions remain: does grazing facilitation during the growth season, or grazing successions through the dry season, translate into an increase in population fitness or abundance or is competition, through the depletion of grass resources during critical periods, more influential on populations and communities?

Hobbs and Swift (1988) found that the beneficial effects of grazing facilitation on forage quality may be compromised by the detrimental effects of grazing competition on the amount of forage available (Hobbs and Swift 1988). For example, facilitation and competition were both found to be operating in an experiment on elk and cattle. Grazing by elk enhanced the digestibility and nitrogen content of forage available to cattle, but also reduced the standing crop of dead perennial grass carried over from year to year, which lowered cattle daily intake rates of dry matter, digestible energy, and nitrogen (Hobbs 1996; Hobbs et al. 1996).

Competition and the effect of herbivores on the quality and quantity of resources are recognized to be related to body size. Brown and Maurer (1986) found that larger organisms account for most of the energy flow from ecosystem resources, and suggest this is due to the advantages of predator evasion, dominance of interspecific aggression, and enhanced ability to use low quality foods. Prins and Olff (1998) suggest the density and

success of smaller herbivores is dependent on the facilitory effects of large herbivores grazing low quality resources.

Alternatively, smaller selective grazing species may have the ability to maintain grasslands at very short grass heights, making them less beneficial to large bulk grazers (Illius and Gordon 1987). High abundances of short grass grazers may maintain grazing lawns, suppressing the recovery by tall grass species, although this pattern tends to occur at a small local scale (Owen-Smith and Cummings 1993).

Larger herbivores can utilize lower quality resources and have a greater diet breadth than smaller species (Owen-Smith 1985; du Toit and Owen-Smith 1989). Also, the local effects of large ungulates can occur over a much larger spatial scale than the local effects of smaller herbivores (Olff and Ritchie 1998). du Toit and Owen-Smith (1989) found that, by feeding productively in habitats less suitable for smaller species, larger species were found to be more evenly spread throughout the environment, whereas, smaller selective feeders, decrease their diet breadth and use less available habitats.

Allometric scaling of incisors among species and digestive strategy has also been shown to be related to resource partitioning among herbivores (Illius and Gordon 1987; Murray and Illius 1996). Through modelling, Illius and Gordon (1987) concluded larger species have greater difficulty gaining their resource needs from short swards than small grazers. In addition, non-ruminants, such as zebra, are less efficient at digestion than ruminants, and compensate with a higher rate of food passage through the gut. Owen-Smith (1985; 1989) used modelling techniques to suggest that zebra may benefit more from eating a wider quality range of food types than similar size ruminants, and may do best in intermediate height grasslands (Owen-Smith 1985).

In feeding studies, zebra have been shown to eat a higher proportion of stems than wildebeest (Gwynne and Bell 1968), and Sinclair (1985) found that, in the dry season zebra showed a preference for taller grass species compared to wildebeest (Sinclair 1985). Murray and Illius (1996) suggest that larger ruminant species and non-ruminants, such as zebra, may thus be competitively excluded if grazing lawns are grazed very low.

However, feeding morphology is expected to override the effects of body size in determining which species has the advantage in grazing the grass sward (Murray and Illius 1996). For example, wildebeest, due to their wide mouths, efficiently feed and prefer short

grass patches, but will usually move in search of fresh re-growth when grass height exceeds 100 to 150 mm in height (Talbot and Talbot 1963). White rhinos and Hippopotamus, with their wide mouths, are able to efficiently graze short grass areas, maintaining these areas at short grass heights. For example, white rhino are able to graze grass to 25 mm in height (Owen-Smith 1988).

Murray and Illius (1996) suggest that grazing lawns may be important in terms of interspecific resource competition between species, where the grazing by some species may negatively affect others through a reduction in grass height or grass quality. For example, Murray and Brown (1993) found that, compared to topi, wildebeest had higher intake rates and could maintain positive energy retention on shorter swards. Zero energy retention was achieved on swards of 30 mm for topi compared to 20 mm for wildebeest. Thus, when grass height is considerably reduced, wildebeest may be able to graze on grazing lawns longer, whereas other species are unable to maintain a positive energy balance (Murray and Brown 1993).

In contrast to wider mouth species, narrow mouth and smaller ungulates, such as topi, hartebeest, sheep and impala, show increased selectivity for high quality sward components (Jarman 1974; Owen-Smith and Novellie 1982; Gordon and Illius 1988; Murray and Brown 1993; O'Reagain 1993). For example, in feeding trials, impala have been shown to select for plant species, such as *Panicum maximum* and *Digitaria macroblephora*, as well as selecting leaves, fruits and flowers over stems (Jarman and Sinclair 1979). Murray and Illius (1996) suggest that increased feeding selectivity may reduce the quality of the swards, making them less beneficial for other species. This may be a mechanism in which narrow mouthed species compete with wider mouthed species, so that interspecific competition is a two way process.

AIM

The main aim of this research is to understand the relative importance of competition and facilitation on the resource use and coexistence of grazing ungulates.

OBJECTIVES

1. To establish the comparative use of grazing lawns by white rhino, impala, wildebeest and zebra.

2. To establish the relationship of grass height, species composition and grass greenness, to the utilization of grazing lawns.

3. To establish the effects of white rhino and impala grazing on the grass height and proportion of green grass of grazing lawns.

4. To establish the effect of white rhino and impala grazing on the utilization of grazing lawns by wildebeest and zebra.

5. To establish the effect of impala grazing on the utilization of medium-tall grass swards

QUESTIONS ADDRESSED

The following major questions are addressed in the thesis: 1) What are the mechanisms of facilitation and competition for grass resources, and where and when do they occur (Chapter Two, Chapter Four)?; 2) What evidence is there that facilitation or competition affect the nutrition and populations of herbivores (Chapter Two)?; 3) Do species partition resources in relation to body size (Chapter Three)?; 4) Do white rhino and impala competitively excluded zebra and wildebeest from grazing lawns in the dry season, through a reduction in grass height (Chapter Four, Chapter Five)?; 5) Do impala

competitively excluded white rhino, zebra and wildebeest from grazing lawns and medium-tall swards through a reduction in green leaf (Chapter Four, Chapter Five)? 6) Do zebra and white rhino facilitate wildebeest and impala in the dry season, by reducing height in tall swards and increasing access to green leaf (Chapter Four)?; and 7) Do white rhino facilitate other herbivores by increasing the quality of grazing lawns in the wet season? (Chapter Five).

Structure of the thesis

This thesis endeavors to understand how grazing herbivores co-exist, with special emphasis on understanding the mechanisms of competition and facilitation over temporal and spatial scales. Please note that Chapter 2 and Chapter 3 were co-authored by Norman Owen-Smith with the aim of publication. The vast majority of these chapters are my work, writing and ideas, and the culmination of numerous drafts. Dr. Owen-Smith contributed in the final drafts helping to edit and tighten the overall story. Chapter Two is a review of facilitation and was published in Oikos in 2002. The first important realization was that the mechanisms of facilitation and competition in terms of temporal and spatial scales were not clearly understood. I was also surprised at how widespread facilitation is believed to be an important structuring force on populations, when there is little evidence in the literature to support this claim. I reviewed the literature and clarified our understanding of the mechanisms of facilitation. I concluded that evidence for facilitation through stimulation of grass re-growth during the growing season appears stronger than that for increased resource access through removal of obstructing grass structures during the dormant season. Facilitation may benefit the nutritional gains obtained by certain species in the short term, but these benefits do not appear to be translated into the expected population consequences. In collaboration with co-author Norman Owen-Smith, we suggested this could be due to seasonal tradeoffs between facilitation and competition, as well as to restrictions on the spatial extent of trophic overlap.

Chapter Three compares the height of grass grazed by the herbivores in relation to current theories of body size, resource partitioning and co-existence. The grass species eaten was determined by locating fresh bites, and the height of the grass species before

grazing was measured. This is the first study to my knowledge to compare grass height choice at such a fine level. It was hypothesized that grass height grazed should increase in height as body size increases. Resource partitioning, by means of different grass heights grazed, may explain how species co-exist despite extensive overlap in ecological requirements.

Chapter Four compares the overlap in grassland use, grass height grazed and grass greenness of swards between the herbivores as the dry season advances. This study also looks at different scales of resource use, such as foraging areas, feeding patches and grass species eaten. This is the first study to my knowledge to compare multiple scales of resources use. It is hypothesized that all herbivores utilize nutritious grazing lawns during times of abundance, but some species such as zebra and wildebeest may be competitively excluded from grazing lawns as the dry season advances. Alternatively, large species and non-ruminants, such a white rhino and zebra, may benefit smaller species by reducing grass height in tall grasslands, removing stem and increasing access to leaves. Finally, selective grazers such as impala, may also competitively exclude other herbivores from medium-tall grasslands by selectively removing green leaf and therefore grass sward quality.

Chapter Five describes an experiment undertaken to understand the relationship between facilitation in the wet season and increased sward quality on grazing lawns by white rhino grazing, versus competitive exclusion for grazing lawns through a reduction in grass height by white rhino grazing in the dry season. We predicted that when white rhino are excluded from grazing lawns, other herbivores will utilize exclosure areas because more grass is available during the dry season. Whereas more herbivores will use control areas (where white rhino graze) in the wet season due to increased productivity and quality of grazing lawns. Chapter 6 is an overview of the main issues and findings of this thesis and suggests future directions for research.

REFERENCES

Anderson, G. D., and Walker, B. H. (1974). Vegetation composition and elephant damage at Sengwa Wildlife Research Area, Rhodesia. J.sthn.Afr.Wildl.Mgmt.Ass., 4, 1-14.

Bailey, D. W., Gross, J. E., Laca, E. A., Rittenhouse, L. R., Coughenour, M. B., Swift, D. M., and Sims, P. L. (1996). Mechanisms that result in large herbivore grazing patterns. Journal of Range Management, 49(5), 386-400.

Bell, R. H. V. (1970). The use of the herb layer by grazing ungulates in the Serengeti. Animal Populations in Relation to their Food Resources, A. Watson, ed., Blackwell Scientific Publications, Oxford, 111-124.

Bell, R. H. V. (1971). A grazing ecosystem in the Serengeti. Scientific American, 224, 86-93.

Brown, J. H., and Maurer, B. A. (1986). Body size, ecological dominance and Cope's rule. Nature, 324, 248-250.

Caughley, G., and Sinclair, A. R. E. (1994). Wildlife Ecology and Management, Blackwell Scientific Publishing, Boston.

de Boer, W. F., and Prins, H. H. T. (1990). Large herbivores that strive mightily but eat and drink as friends. Oecologia, 82, 264-274.

du Toit, J. T., and Owen-Smith, N. (1989). Body size, population metabolism, and habitat specialization among large African herbivores. American Naturalist, 133(5), 736-740.

Dublin, H. T., Sinclair, A. R. E., Boutin, S., Anderson, E., Jago, M., and Arcese, P. (1990). Does competition regulate ungulate populations? Further evidence from Serengeti, Tanzania. Oecologia, 82, 283-288.

Fritz, H., de Garine-Wichatitsky, M., and Letessier, G. (1996). Habitat use by sympatric wild and domestic herbivores in an African savanna woodland: the influence of cattle spatial behaviour. Journal of Applied Ecology, 33, 589-598.

Fryxell, J. M. (1991). Forage quality and aggregation by large herbivores. American Naturalist, 138(2), 478-498.

Fryxell, J. M., Greever, J., and Sinclair, A. R. E. (1988). Why are migratory ungulates so abundant? American Naturalist, 131(6), 781-798.

Fryxell, J. M., and Sinclair, A. R. E. (1988). Seasonal migration by white-eared kob in relation to food resources. African Journal of Ecology, 26, 17-31.

Gause, G. F. (1934). Struggle for Existence, Hafner, New York.

Gordon, I. J. (1988). Facilitation of red deer grazing by cattle and its impact on red deer performance. Journal of Applied Ecology, 25, 1-10.

Gordon, I. J., and Illius, A. W. (1988). Incisor arcade structure and diet selection in ruminants. Functional Ecology, 2, 15-22.

Gwynne, M. D., and Bell, R. H. V. (1968). Selection of vegetation components by grazing ungulates in the Serengeti National Park. Nature, 220, 390-393.

Hobbs, N. T. (1996). Modification of ecosystems by ungulates. Journal of Wildlife Management, 60(4), 695-713.

Hobbs, N. T., Baker, D. L., Bear, G. D., and Bowden, D. C. (1996). Ungulate grazing in sagebrush grassland: mechanisms of resource competition. Ecological Applications, 6(1), 200-217.

Hobbs, N. T., and Swift, D. M. (1988). Grazing in herds: when are nutritional benefits realized? American Naturalist, 131, 760-764.

Illius, A. W., and Gordon, I. J. (1987). The allometry of food intake in grazing ruminants. Journal of Animal Ecology, 56, 989-999.

Jarman, P. J. (1974). The social organization of antelope in relation to their ecology. Behaviour, 48, 215-266.

Jarman, P. J., and Sinclair, A. R. E. (1979). Feeding strategy and the pattern of resource partitioning in ungulates. Serengeti: Dynamics of an Ecosystem, A. R. E. Sinclair and M. Norton-Griffiths, eds., University of Chicago Press, Chicago.

MacArthur, R. H. (1972). Geographical Ecology, Harper and Row, New York.

McNaughton, S. J. (1976). Serengeti migratory wildebeest: facilitation of energy flow by grazing. Science, 191, 92-94.

McNaughton, S. J. (1979). Grazing as an optimization process: grass-ungulates relationships in the Serengeti. American Naturalist, 113, 691-703.

McNaughton, S. J. (1984). Grazing lawns: animals in herds, plant form, and co-evolution. American Naturalist, 124(6), 863-888.

McNaughton, S. J. (1985). Ecology of a grazing ecosystem: the Serengeti. Ecological Monographs, 55(3), 258-294.

Melton, D. A. (1987). Habitat selection and resource scarcity. South African Journal of Science, 83, 646-651.

Murray, M. G., and Brown, D. (1993). Niche Separation of grazing ungulates in the Serengeti: an experimental test. Journal of Animal Ecology, 62, 380-389.

Murray, M. G., and Illius, A. W. (1996). Multi-species grazing in the Serengeti. The Ecology and Management of Grazing Systems, J. Hodgson and A. W. Illius, eds., CAB International, 247-272.

Olff, H., and Ritchie, M. E. (1998). Effects of herbivores on grassland plant diversity. TREE, 17(7), 261-265.

O'Reagain, P. J. (1993). Plant structure and the acceptability of different grasses to sheep. Journal of Range Management, 46(3), 232-236.

O'Reagain, P. J., and Schwartz, J. (1995) Coping with spatial and temporal variability: dietary selection and foraging strategies of animals on rangeland. .

Owen-Smith. (1973). The Behavioural Ecology of the White Rhinoceros, , University of Wisconsin.

Owen-Smith, N. (1985). Niche separation among African ungulates. Species and Speciation, E. S. Vrba, ed., Transvaal Museum Monograph No. 4, Pretoria, 167-171.

Owen-Smith, N. (1988). Megaherbivores: The influence of very large body size on ecology, Cambridge University Press, Cambridge.

Owen-Smith, N. (1989). Morphological factors and their consequences for resource partitioning among African savanna ungulates: a simulation modelling approach. Patterns and Structure of Mammalian Communities, D. W. Morris, Z. Abramsky, B. J. Fox, and M. R. Willig, eds., Texas Tech University Press, 155-165.

Owen-Smith, N. (2002). Adaptive Herbivore Ecology: From Resources to Populations in Variable Environments. Cambridge University Press.

Owen-Smith, N., and Cooper, S. M. (1987). Assessing food preferences of ungulates by acceptability indices. Journal of Wildlife Management, 51(2), 372-378.

Owen-Smith, N., and Cummings, D. H. M. (1993). Comparative foraging strategies of grazing ungulates in African savanna grasslands. Proceedings of the XVII International Grassland Conference, 691-698.

Owen-Smith, N., and Novellie, P. (1982). What should a clever ungulate eat? American Naturalist, 119(2), 151-177.

Prins, H. H. T., and Olff, H. (1996). Species richness of African grazer assemblages: towards a functional explanation. Dynamics of Tropical Communities, D. M. Newbury, H. H. T. Prins, and N. D. Brown, eds., Blackwell Science, 449-490.

Putman, R. J. (1996). Competition and Resource Partitioning in Temperate Ungulate Assemblies, Chapman and Hall, London.

Root, R. (1967). The niche exploitation pattern of the blue-grey gnatcatcher. Ecological Monographs, 37, 317-350.

Schoener, T. W. (1974). Resource partitioning in ecological communities. Science, 185, 27-39.

Schoener, T. W. (1983). Field experiments in interspecific competition. American Naturalist, 122, 240-285.

Schoener, T. W. (1986). Resource Partitioning. Community Ecology: Pattern and Process, J. Kikkawa and D. J. Anderson, eds., Blackwell Scientific Publications, 91-126.

Senft, R. L., Coughenour, M. B., Bailey, D. W., Rittenhouse, L. R., Sala, O. E., and Swift, D. M. (1987). Large herbivore foraging and ecological hierarchies. Bioscience, 37(11), 789-799.

Sinclair, A. R. E. (1985). Does interspecific competition or predation shape the African ungulate community? Journal of Animal Ecology, 54, 899-918.

Sinclair, A. R. E., and Norton-Griffiths, M. (1982). Does competition or facilitation regulate migrant ungulate populations in the Serengeti? A test of hypotheses. Oecologia, 53, 364-369.

Talbot, L. M., and Talbot, M. H. (1963). The wildebeest in western Masailand, East Africa. Wildlife Monographs(12).

Tilman, D. (1982). Resource competition and community structure, Princeton University Press, Princeton, New Jersey, USA.

Vesey-Fitzgerald, D. F. (1960). Grazing succession among East African game animals. Journal of Mammalogy, 41, 161-172.

Walker, B. H. (1976). An approach to the monitoring of changes in the composition and utilization of woodland and savanna vegetation. S.Afr.J.Wildl.Res., 1-7.

CHAPTER TWO

Facilitation versus competition in grazing herbivore assemblages

By Randal Arsenault and Norman Owen-Smith
- published in Oikos 97:313-318 (2002

ABSTRACT

The importance of facilitation versus competition in structuring herbivore species assemblages is a critical issue in theoretical ecology as well as for practical wildlife management. This paper examines the evidence for facilitation and clarifies our understanding in relation to the mechanisms and the spatial and temporal scales where they occur. Evidence for facilitation through stimulation of grass regrowth during the growing season appears stronger than that for increased resource access through removal of obstructing grass structures during the dormant season. Although facilitation may benefit the nutritional gains obtained by certain species in the short term, these benefits do not appear to be translated into the expected population consequences. We suggest this could be due to seasonal tradeoffs between facilitation and competition, as well as to restrictions on the spatial extent of trophic overlap.

INTRODUCTION

Trophic interactions among large mammalian herbivores are mediated largely through their grazing and browsing impacts on vegetation (Vesey-Fitzgerald 1960; Bell 1970; Eltringham 1974; Owen-Smith 1985; Murray and Illius 1996; Murray and Illius 2000). Competition may arise where one species reduces shared food resources below the level that can be exploited efficiently by another species (Illius and Gordon 1987; Murray and Illius 1996; Prins and Olff 1998). Alternatively, by reducing grass biomass one

species may benefit another by facilitating access to forage of a suitable height or quality (Vesey-Fitzgerald 1960; Bell 1970; Bell 1971; McNaughton 1976). The relative importance of these two processes in structuring species assemblages remains unclear. Current understanding is that competition is reduced primarily through distinctions in body size, and secondarily through adaptations in trophic morphology, leading to differential preferences for grass height and forage quality (Bell 1970; Jarman 1974; Demment and Van Soest 1985; Owen-Smith 1985; Illius and Gordon 1987; Owen-Smith 1989; Prins and Olff 1998). Large species have the ability to utilize high food biomass that is low in quality (Bell 1971; Jarman 1974; Demment and Van Soest 1985; Illius and Gordon 1987). Small species require high forage quality, but can tolerate low food biomass levels. Small species may thus benefit from the grazing impacts of larger species, and potentially out compete the latter when food supplies become reduced (Illius and Gordon 1987; Gordon and Illius 1989). Furthermore, by selectively grazing on green leaf in taller swards, smaller or more narrow-muzzled species also have the ability to deplete this component to the detriment of forage quality for larger species (Murray and Illius 1996; Murray and Illius 2000).

While the joint importance of competition and facilitation in structuring large herbivore assemblages is widely recognised in textbooks and reviews (Owen-Smith 1989; Ricklefs 1990; Krebs 1994; Putman 1996; Dobson 1998; Prins and Olff 1998; Murray and Illius 2000), empirical evidence for effects at the population level remains meagre. Hairston et al. (1960) proposed, provocatively, that the herbivore trophic level is generally predator-limited rather than food-limited, noting the widespread prevalence of much uneaten green vegetation (Hairston 1960). This viewpoint has been firmly rejected for large mammalian herbivores, on the basis that forage of a suitable quality becomes severely limited seasonally (Sinclair 1975). Moreover, herbivore biomass is closely correlated with annual rainfall, and hence with vegetation production (Coe et al. 1976; Fritz and Duncan 1994). But why then is convincing evidence for trophic influences, whether facilitatory or competitive, on population abundance and hence community composition so elusive? How is it that the big species survive, and indeed dominate the biomass within large herbivore assemblages (Bell 1982; Owen-Smith 1988; du Toit and Owen-Smith 1989), despite being supposedly the inferior competitors?

Mere overlap in resources utilized by individual animals does not necessarily constitute competition. The outcome depends on the extent to which these resources limit population abundance (Wiens 1989; Putman 1996). Grass resources may appear to be superabundant during the growing season, but only a fraction of this potential food may be nutritionally acceptable and accessible (Wilmshurst et al. 1995; Prins and Olff 1998). During the non-growing season, grasses become dormant and forage is progressively depleted. At this time of the year herbivores of different species tend to segregate into distinct habitats, or concentrate on different resource types (Jarman and Sinclair 1979; Owen-Smith 1982; Owen-Smith and Novellie 1982; Gordon and Illius 1989). But such segregation does not necessarily imply a lack of competition, as one species may be excluded from habitats or resource components that it would have otherwise utilized but for the feeding impacts of another (Rosenzweig 1981). From a broader perspective, we may observe only the "ghost of competition" (Connell 1980) in the form of assemblages of species that compete weakly or only intermittently, because strong competitors were eliminated in the evolutionary past.

We suggest that greater clarity about the relative roles of competition and facilitation in structuring large herbivore assemblages could be obtained if more recognition was given to (1) the effective mechanisms through which these processes operate, (2) contrasting effects during different seasons, and (3) spatial heterogeneity in the available resources. We explain our case, and present supporting evidence, below, with a focus on facilitation in particular. We distinguish between feeding facilitation, population facilitation and habitat facilitation, outline potential seasonal tradeoffs between facilitation and competition, and suggest how this perspective helps explain observed patterns of spatial partitioning among herbivore species.

FEEDING FACILITATION

Feeding facilitation may arise in two different ways: (1) when grazing by one species makes more grass accessible to another species, e.g. by reducing grass height and removing stems (Vesey-Fitzgerald 1960; Bell 1970; Bell 1971), or (2) when grazing by one species stimulates grass regrowth, thereby enhancing the nutritional quality of forage for another species (Vesey-Fitzgerald 1974; McNaughton 1976; Gordon and Illius 1988).

Increased resource access

Facilitation through increased access to resources was described qualitatively by Vesey-Fitzgerald (1960), in terms of a grazing succession. His observations were made in tall floodplain grasslands in the Rukwa Valley in Tanzania, where trampling and feeding by elephants (*Loxodonta africana*) exposed medium-height grasses to buffalo (*Syncerus caffer*), which in turn generated shorter grass exploited by topi (*Damaliscus lunatus*).

Further evidence supporting the grazing succession concept was provided by Bell (1970; 1971), who studied the distribution of resident buffalo, zebra (*Equus burchelli*), wildebeest (*Connochaetes taurinus*), topi and Thomson's gazelle (*Gazella thomsonii*), across the catenary sequence of grasslands in the western Serengeti. All species concentrated on the highest ground during the wet season, where short grasses offering the best quality forage dominated. Towards the end of the wet season, species moved in order of decreasing body size towards lower ground, where medium-tall but poorer quality grasses occurred (with the exception of topi, which left before the larger wildebeest). Furthermore, Bell (1971) observed migratory populations of three of these species (zebra, wildebeest, Thomson's gazelle) moving through his study area, and recorded that they likewise moved in order of body size in relation to changes in grass height.

Recent authors have questioned Bell's (1970; 1971) interpretation of these patterns of species association as representing grazing facilitation (Sinclair and Norton-Griffiths 1982; Illius and Gordon 1987; de Boer and Prins 1990; Putman 1996; Prins and Olff 1998). The movement of larger species from the upper catena could readily be explained as a consequence of grass height reduction, once the grass had stopped growing. (Illius and Gordon 1987). Whether the smaller species benefited in any way from the grazing impacts of the larger species was unclear.

Although movements of the migratory populations of zebra, wildebeest and Thomson's gazelle appeared to be associated with changing grass height, substantial numbers of resident wildebeest remained in the area throughout this time. The reduction in grass height that occurred before the arrival of migratory wildebeest could have been due to the grazing of resident wildebeest, rather than that of migrant zebra. Furthermore,

subsequent observations failed to support Bell's contention that the migratory wildebeest followed behind the zebra in their migrations (Sinclair and Norton-Griffiths 1982; Sinclair 1985).

Increased quality of resources

McNaughton (1976) provided convincing evidence that Thomson's gazelle were attracted to areas where prior grazing by wildebeest improved the quality of the grass sward on the Serengeti plains. Concentrations of migratory wildebeest removed 85% of the green biomass of a *Themeda-Pennisetum* tall grassland over a 2-3 week period. This stimulated leafy grass regrowth and increased the green biomass concentration. In contrast, green biomass declined as grass became senescent in nearby areas protected from wildebeest grazing. Thomson's gazelle maintained their preference for areas previously grazed by wildebeest up to 6 months after the passage of the wildebeest, well into the dry season. McNaughton (1984) demonstrated furthermore that grassland productivity, as well as the green leaf concentration within swards, was enhanced by quite high levels of grazing. However, Wilmshurst and Fryxell (unpublished manuscript) found that there was a subsequent competitive impact on gazelles, as a result of the reduction in grass standing crop brought about by the grazing impact of the wildebeest.

Working on the Isle of Rum, Scotland, Gordon (1988) found that areas grazed by cattle (*Bos taurus*) during winter had a significantly higher standing crop of green vegetation in e spring, and had proportionately more green than dead material, than areas protected from cattle grazing. He observed that red deer (*Cervus elaphus*) in spring preferred to feed in areas that had been grazed previously by cattle during the preceding winter.

Hobbs et al. (1996) investigated the effects of winter grazing by elk (*Cervus elaphus canadensis*) on cattle grazing during spring and early summer in sagebrush grasslands in Colorado. The study was conducted experimentally using exclosures with elk stocked at different densities. Prior grazing by elk enhanced the nitrogen content and digestibility of the forage available to cattle, and the nitrogen content of cattle diets. However, under high elk stocking density, the improvement in dietary quality was

counterbalanced by a substantial reduction in the daily dry matter, digestible energy and protein intake of the cattle, as a consequence of reduced carryover of dead perennial grass from year to year (Hobbs et al. 1996). Notably, spatial partitioning in patch use was precluded.

In summary, evidence suggests that feeding facilitation can occur through the improved forage quality of grass regrowth, rather than simply through increased resource access through the removal of obstructing grass structures. Such facilitation would therefore occur during the growing season for the vegetation.

POPULATION FACILITATION

Both Vesey-Fitzgerald and Bell implied that feeding facilitation would translate into improved population performance for species grazing later in the succession. Vesey-Fitzgerald (1960) suggested that the presence of elephants promoted greater numbers of medium-sized herbivores in the Lake Rukwa region, while Bell (1970) postulated that a decline in zebra abundance in the Serengeti ecosystem could lead to a reduction in wildebeest numbers. Changes in herbivore populations in the Serengeti over the past 25 years have not supported the latter expectation. Wildebeest have increased almost four-fold, while zebra numbers have remained stationary (Sinclair and Norton-Griffiths 1982; Dublin et al. 1990; Putman 1996), indicating little or no interdependency.

Although feeding facilitation was demonstrated to benefit Thomson's gazelle in the short term (McNaughton 1976), the large increase in wildebeest in the Serengeti ecosystem has also not resulted in an increase in the Thomson's gazelle population (Sinclair and Norton-Griffiths 1982; Dublin et al. 1990).

Following the recent elimination of buffalo from the northern and western regions of the Serengeti National Park through poaching, topi, impala (*Aepyceros melampus*), and possibly oribi (*Ourebia ourebi*), have increased in abundance. Thus competition rather than facilitation is suggested, although the population changes of the smaller species could also be due to release from predation (Sinclair 1985).

On the Isle of Rum, Gordon (1988) found that red deer produced more calves per female after 1971, when cattle were introduced, than over the period from 1957 to 1971

while cattle were absent. Improved calf production could potentially lead to higher population abundance, but this was not demonstrated.

In another temperate zone study, Putman (1996) assessed evidence for competition or facilitation within a species assemblage including cattle, ponies (*Equus caballus*), red deer, sika deer (*Cervus nippon*), fallow deer (*Dama dama*), and roe deer (*Capreolus capreolus*) in the New Forest, England. Changes in fallow deer numbers were negatively related to the numbers of cattle and ponies pastured in the forest in the previous year, clearly negating any population-level facilitation from these larger grazers.

Although facilitation has been widely accepted as an important structuring force of grazing ungulate communities, we found no evidence that feeding facilitation has anywhere been translated into an increase in population abundance.

HABITAT FACILITATION

The vegetation changes induced by the feeding and destructive impacts of megaherbivores, (species weighing >1000 kg as adults) can alter habitat structure, to the benefit or detriment of other species. Notably, the cascade of extinctions throughout northern Eurasia and the Americas during the late Pleistocene encompassed not only all megaherbivores, but also many medium-sized mammalian herbivores less vulnerable to human hunting pressure (Alroy 2001). This suggests that the medium sized species may have benefited from the habitat structure promoted by megaherbivore impacts on vegetation (Owen-Smith 1987).

The propensity of elephants to transform savanna woodlands into either open parkland or shrubland, depending on underlying soil type, is well known (Laws 1970; Bell 1981). The vast increase in elephants in the Tsavo region of Kenya during the 1960s, and consequent opening of dense shrubland, was followed by increases in the abundance of grazers like oryx (*Oryx gazella*) and zebra, while browsers such as lesser kudu (*Tragelaphus imberbis*) and gerenuk (*Litocranius walleri*) declined (Parker 1983). Declines by some grazing ungulates, plus increases by browsers, in the Hluhluwe Game Reserve in South Africa were attributed to habitat thickening following the extermination of elephants a century earlier (Owen-Smith 1989).

Grazing hippopotamus (*Hippopotamus amphibius*) and white rhinoceros (*Ceratotherium simum*) can likewise transform tall grass grasslands into extensive grazing lawns (Olivier and Laurie 1974; Owen-Smith 1988). Elimination of hippos from the Mweya Peninsula region of the Queen Elizabeth National Park, Uganda, was followed by a substantial increase in elephant, buffalo and waterbuck (*Kobus ellipsiprymnus*), species favouring tall grass, after the lakeshore grassland had recovered from the short state maintained by hippo grazing (Eltringham 1974). Following the recovery of the hippo population, numbers of these three species reportedly declined in this region. The increase in white rhino abundance in the Hluhluwe-Umfolozi Park in South Africa was associated with declines by reedbuck (*Reduca arundinum*) and waterbuck, both dependent on tall grass (Owen-Smith 1988). Species preferring short grass, specifically wildebeest, zebra, impala and warthog *(Phacochoerus aethiopicus*) have maintained or increased their abundance.

Wild ungulates the size of buffalo (ca.600 kg) and smaller do not appear responsible for large scale habitat changes in African savanna ecosystems, except in situations were predators were eliminated, movements confined by fencing to small areas, or locally in the vicinity of water points (Cumming 1982). This generalization does not apply to domestic cattle stocked at high densities by sedentary pastoralists (du Toit and Cummings 1999). Nevertheless, hare (*Lepus europaecus*) browsing was found to slow the succession of shrubs for > 25 yrs, benefiting the grazing of Brent geese (*Branta bernicula bernicula*) (van der Wal et al. 2000).

Hence, there seems to be sufficient evidence demonstrating population responses by herbivores in response to facilitative habitat alteration by other species, in some situations. However, habitat facilitation is not restricted to the major vegetation impacts caused by the very largest herbivores.

TEMPORAL TRADEOFFS

Beneficial effects of grazing impacts on grass production, green leaf concentrations, sward bulk density and nitrogen cycling have been convincingly demonstrated (McNaughton 1984; McNaughton 1985). The consequent enhancement of

energy flow through improved forage quality may have contributed to the high abundance of wildebeest in the Serengeti ecosystem, and of white rhinos in the Hluhluwe-Umfolozi Park, through their own grazing impacts (i.e. self facilitation) (Owen-Smith 1988). Why have positive consequences for population levels of other large herbivore species not been found?

One possible explanation is the confounding effect of predation, where for example higher wildebeest numbers in the Serengeti promote greater predator abundance, thereby having a negative impact on the population levels of zebra and Thomson's gazelle (McNaughton 1984; McNaughton 1985; Sinclair 1985).

An alternative explanation that we propose involves the seasonal trade-off between facilitation and competition. The grazing impacts of white rhino and wildebeest promote improved grass quality for other grazing herbivores during the wet season, enhancing reproductive performance. However, as a consequence less grass remains to support the latter species through the dry season, restricting population levels.

Klein (1965) noted that for deer (*Odocoilus spp.*) in North America, population abundance is determined primarily by the amount of food remaining during late winter, affecting over-winter survival. In contrast, food quality during early summer governs individual growth and physical condition, and consequently reproductive success (Klein 1965). Owen-Smith (1990) found that the calving success of greater kudus under African savanna conditions was determined largely by rainfall over the preceding wet season, possibly promoting the production of high quality forage in the form of forbs. On the other hand, the overall population density of browsers like kudus is determined largely by the amount of forage retained through the late dry season (Owen-Smith 2002).

Hence, we suggest that interspecific competition predominates during the dormant (winter or dry) season, when forage of adequate quality becomes progressively depleted. The effects of such competition can be ameliorated by feeding facilitation arising from enhanced food quality during the growing season, improving recruitment success. The overall demographic consequence depends on the balance between these temporal tradeoffs. Thus, although evidence for either feeding facilitation or competition may be found at one time of the year, the anticipated population consequences need not necessarily follow. We do not exclude the possibility that "apparent competition"

mediated through shared predators may be an additional influence. Susceptibility to predation can, however, be dependent largely on nutritional status (Sinclair and Arcese 1995).

SPATIAL PARTITIONING OF RESOURCES

Trophic interactions among herbivore species of differing body size take place within a complex spatial mosaic, most especially for grazing ungulates within African savannas (McNaughton 1983; 1989). Small species could potentially out-compete larger species within the habitat types they occupy, through their feeding effects on resource abundance or quality during the dormant season. However, small herbivores tend to be localized in their distribution, because of their need for high-quality forage, while large species forage less selectively across a range of vegetation types (du Toit and Owen-Smith 1989). The effect of competition by smaller species on the forage quantity and quality obtained by larger species is thus restricted in its spatial extent. Moreover, because large species forage through the high quality patches favoured by small species while sufficient food remains on offer, they reduce the amount of food left to support smaller species through the dormant season. Hence, competition is a two-way process, but somewhat localized in its occurrence.

CONCLUSIONS

Feeding facilitation arises mainly during the growing season, when grazing by larger species may stimulate vegetation regrowth and hence temporarily improve forage quality for other species. Improved reproductive success may result. Counterbalancing this is a reduction in the amount of forage remaining to support populations through the dormant season, with mortality heightened as a result. While competition and facilitation may be manifested through short term consequences for foraging efficiency, the effects on population dynamics may be suppressed through seasonal tradeoffs and spatial localization. The population outcome depends on the overall regime over the annual cycle. We conclude that feeding facilitation in the growing season can act to ameliorate the

exploitative competition that comes into operation during the dormant season, and that this is an important mechanism promoting species coexistence within grazing herbivore assemblages.

Acknowledgements –

We acknowledge helpful comments, suggestions and criticisms on previous drafts of this manuscript from Andrew Illius, John Wilmshurst, Iain Gordon and Johan du Toit, and in review by Herbert Prins and John Fryxell.

REFERENCES

Alroy, J. (2001). A multispecies overkill simulation of the end-Pleistocene megafaunal mass extinction. Science 292:1893-1896.

Bell, R. H. V. (1970). The use of the herb layer by grazing ungulates in the Serengeti. - In: Watson, A. (eds.), Animal Populations in Relation to their Food Resources. Blackwell Scientific Publications, Oxford, pp. 111-124.

Bell, R. H. V. (1971). A grazing ecosystem in the Serengeti. Scientific American 224:86-93.

Bell, R. H. V. (1981). An outline of a management plan for Kasunga National Park, Malawi. In: Jewel, P. A., Holt, S. and Hart, D. (eds.), Problems in Management of Locally Abundant Wild Mammals, pp. 69-89.

Bell, R. H. V. (1982). The effect of soil nutrient availability on community structure in African ecosystems. In: Huntley, B. J. and Walker, B. H. (eds.), Ecology of Tropical Savannas. Springer-Verlag, Berlin, pp. 193-216.

Coe, M. J., Cummings, D. H. M. and Phillipson, J. (1976). Biomass and production of large herbivores in relation to rainfall and primary production. Oecologia 22:341-354.

Connell, J. H. (1980). Diversity and coevolution of competitors, or the ghost of competition past. Oikos 35:131-138.

Cumming, D. H. M. (1982). The influence of large herbivores on savanna structure in Africa. In: Huntley, B. J. and Walker, B. H. (eds.), Ecology of Tropical Savannas. Springer-Verlag, Berlin, Vol. 42, pp. 217-245.

de Boer, W. F. and Prins, H. H. T. (1990). Large herbivores that strive mightily but eat and drink as friends. Oecologia 82:264-274.

Demment, M. W. and Van Soest, P. J. (1985). A nutritional explanation for body size patterns of ruminant and non ruminant herbivores. American Naturalist 125:641-672.

Dobson, S. I. 1998. Ecology. Oxford University Press.

du Toit, J. T. and Cummings, D. H. M. (1999). Functional significance of ungulate diversity in African savannas and the ecological implications of the spread of pastoralists. Biodiversity and Conservation 8:1643-1661.

du Toit, J. T. and Owen-Smith, N. (1989). Body size, population metabolism, and habitat specialization among large African herbivores. American Naturalist 133:736-740.

Dublin, H. T., Sinclair, A. R. E., Boutin, S., Anderson, E., Jago, M. and Arcese, P. (1990). Does competition regulate ungulate populations? Further evidence from Serengeti, Tanzania. - Oecologia 82:283-288.

Eltringham, S. K. (1974). Changes in the large mammal community of Mweya Peninsula, Rwenzori National Park, Uganda, following removal of hippopotamus. Journal of Applied Ecology 11:855-865.

Fritz, H. and Duncan, P. (1994). On the carrying capacity for large ungulates of African savanna ecosystems. Proc. R. Soc. Lond. B. 256:77-82.

Gordon, I. J. and Illius, A. W. (1988). Incisor arcade structure and diet selection in ruminants. Functional Ecology 2:15-22.

Gordon, I. J. and Illius, A. W. (1989). Resource partitioning by ungulates on the Isle of Rhum. Oecologia 79:383-389.

Hairston, N. G. Smith, F.E. and Slobodkin, L.B. (1960). Community structure, population control and competition. American Naturalist 94:421-425.

Hobbs, N. T., Baker, D. L., Bear, G. D. and Bowden, D. C. (1996). Ungulate grazing in sagebrush grassland: mechanisms of resource competition. Ecological Applications 6:200-217.

Illius, A. W. and Gordon, I. J. (1987). The allometry of food intake in grazing ruminants. Journal of Animal Ecology 56:989-999.

Jarman, P. J. (1974). The social organization of antelope in relation to their ecology. Behaviour 48:215-266.

Jarman, P. J. and Sinclair, A. R. E. (1979). Feeding strategy and the pattern of resource partitioning in ungulates. In: Sinclair, A. R. E. and Norton-Griffiths, M. (eds.), Serengeti: Dynamics of an Ecosystem. University of Chicago Press, Chicago.

Klein, D. R. (1965). Ecology of deer range in Alaska. Ecological Monographs 35:259-284.

Krebs, C. J. (1994). Ecology. Harper Collins College Publishers.

Laws, R. M. (1970). Elephants as agents of habitat and landscape change in East Africa. Oikos 21:1-15.

McNaughton, S. J. (1976). Serengeti migratory wildebeest: facilitation of energy flow by grazing. Science 191:92-94.

McNaughton, S. J. (1983). Compensatory plant growth as a response to herbivory. Oikos 40:329-336.

McNaughton, S. J. (1984). Grazing lawns: animals in herds, plant form, and coevolution. American Naturalist 124:863-888.

McNaughton, S. J. (1985). Ecology of a grazing ecosystem: the Serengeti. Ecological Monographs 55:258-294.

McNaughton, S. J. (1989). Interaction of the plants of the field layer with large herbivores. Symp. Zool. Soc. Lond 61:15-29.

Murray, M. G. and Illius, A. W. (1996). Multispecies grazing in the Serengeti. In: Hodgson, J. and Illius, A. W. (eds.), The Ecology and Management of Grazing Systems. CAB International, pp. 247-272.

Murray, M. G. and Illius, A. W. (2000). Vegetation modification and resource competition in ungulates. Oikos 89: 501-508.

Olivier, R. C. D. and Laurie, W. A. (1974). Habitat utilization of the hippopotamus in the Mara River. East African Wildlife Journal 12:249-272.

Owen-Smith, N. (1982). Factors influencing the consumption of plant products by large herbivores. - In: Huntley, B. J. and Walker, B. H. (eds.), Ecology of Tropical Savannas. Springer-Verlag, Berlin, pp. 359-404.

Owen-Smith, N. (1985). Niche separation among African ungulates. In: Vrba, E. S. (eds.), Species and Speciation. Transvaal Museum Monograph No. 4, Pretoria, pp. 167-171.

Owen-Smith, N. (1987). Pleistocene extinctions: the pivotal role of megaherbivores. - Paliobiology 13:351-362.

Owen-Smith, N. (1988). Megaherbivores: The influence of very large body size on ecology. Cambridge University Press, Cambridge.

Owen-Smith, N. (1989). Morphological factors and their consequences for resource partitioning among African savanna ungulates: a simulation modelling approach. In: Morris, D. W., Abramsky, Z., Fox, B. J. and Willig, M. R. (eds.), Patterns and Structure of Mammalian Communities. Texas Tech University Press, pp. 155-165.

Owen-Smith, N. (2002). Adaptive Herbivore Ecology: From Resources to Populations in Variable Environments. Cambridge University Press.

Owen-Smith, N. and Novellie, P. (1982). What should a clever ungulate eat? American Naturalist 119:151-177.

Parker, I. S. C. (1983). The Tsavo story: an ecological case history. In: Owen-Smith, N. (eds.), Mammals in African Conservation Areas, pp. 37-50.

Prins, H. H. T. and Olff, H. (1998). Species richness of African grazer assemblages: towards a functional explanation. In: Newbury, D. M., Prins, H. H. T. and Brown, N. D. (eds.), Dynamics of Tropical Communities. Blackwell Science, pp. 449-490.

Putman, R. J. (1996). Competition and Resource Partitioning in Temperate Ungulate Assemblies. Chapman and Hall, London.

Ricklefs, R. E. (1990). Ecology. W.H. Freeman and Company.

Rosenzweig, M. L. (1981). A theory of habitat selection. Ecology 62:327-335.

Sinclair, A. R. E. (1975). The resource limitation of trophic levels in tropical grassland ecosystems. Journal of Animal Ecology 44:497-520.

Sinclair, A. R. E. (1985). Does interspecific competition or predation shape the African ungulate community? Journal of Animal Ecology 54:899-918.

Sinclair, A. R. E. and Arcese, P. (1995). Population consequences to predation - sensitive foraging: the Serengeti wildebeest. Ecology 76:882-891.

Sinclair, A. R. E. and Norton-Griffiths, M. (1982). Does competition or facilitation regulate migrant ungulate populations in the Serengeti? A test of hypotheses. Oecologia 53:364-369.

van der Wal, R., van Wijnen, H., van Wieren, S., Beucher, O. and Bos, D. (2000). On facilitation between herbivores: how Brent geese profit from brown hares. Ecology 81:969-980.

Vesey-Fitzgerald, D. F. (1960). Grazing succession among East African game animals. Journal of Mammalogy 41:161-172.

Vesey-Fitzgerald, D. F. (1974). Utilization of the grazing resources by buffaloes in the Arusha National Park, Tanzania. East African Wildlife Journal 12:107-134.

Wiens, J. A. (1989). The Ecology of Bird Communities. Volume 1: Foundations and Patterns. Cambridge University Press, Cambridge.

Wilmshurst, J. F., Fryxell, J. M. and Hudson, R. J. (1995). Forage quality and patch choice by wapiti. Behavioural Ecology 6:209-217.

CHAPTER THREE

Resource partitioning by grass height among grazing ungulates does not follow body size relation

Randal Arsenault and Norman Owen-Smith
Centre for African Ecology, School of Animal, Plant and Environmental Sciences, University of Witwatersrand, Private Bag 3, WITS 2050, South Africa

Summary

We compared the grass height grazed by white rhino, wildebeest, zebra and impala through the dry season months in the Hluhluwe-iMfolozi Park in South Africa. We expected that the grass height favoured would increase with the body size of the herbivore species, as suggested from past studies of resource partitioning among large mammalian herbivores. Instead we found that the largest of these species, white rhino, concentrated on the shortest grass, while the smallest species, impala, favoured grass heights intermediate between those grazed by wildebeest and zebra. Results suggest that the scaling of mouth width relative to body size, and hence metabolic demands, is the primary factor governing grass height selection, rather than body size alone. Hence grazing successions governed by body size differences may not be a typical feature of their ecology, contrary to past suggestions. Furthermore, there was considerable overlap in grass height grazed among these four species, indicating that niche separation by grass height is inadequate alone to explain their coexistence. More attention needs to be paid to other aspects such as the grass species selected and habitat structure favoured.

Key words: Body size – Grazing ungulates – Grass height – Resource partitioning

Allometric relations between body size, metabolic requirements and the morphological features influencing food intake are believed to govern distinctions in the food niche of large mammalian herbivores (Bell 1970; 1971; Jarman 1974; Owen-Smith 1985; Illius and Gordon 1987; Gordon and Illius 1988). The prevalent view is that past interspecific competition has lead to differential selection for grass height and forage quality among grazing herbivores dependent largely on body size and digestive system (Murray and Illius 1996; Prins and Olff 1998). Specific metabolic requirements scale with body mass to the power minus one quarter ($M^{-1/4}$), while gut capacity is isometric with body mass, implying that larger herbivores can tolerate poorer quality forage than smaller species (Demment and Van Soest 1985). Species with digestive processing taking place via hindgut fermentation show a faster passage rate than ruminants with foregut fermentation, enabling them to subsist on less digestible forage than ruminants of similar body size (Duncan et al. 1990).

Furthermore, a grazing succession has been described for the Serengeti region of Tanzania, with the largest species moving away first as the better quality but shorter grass growing in uplands becomes depleted (represented here by African buffalo *Syncerus caffer* and plains zebra *Equus burchelli*), followed by other grazers in order of their body size (specifically wildebeest *Connochetes taurinus* then Thomson's gazelle *Gazella thomsoni*) (Bell 1970, 1971; see also Vesey-Fitzgerald 1960). This pattern has been interpreted as an example of facilitation, with the reduction in grass height brought about by larger species improving grazing conditions for smaller herbivores (McNaughton 1976; see also Arsenault and Owen-Smith 2002).

Following from Hutchinson's (1950) work on body size and niche partitioning, Prins and Olff (1998) contended that potential competition is pervasive among grazing herbivores, such that species of similar body size rarely occur together. They suggested further that some minimal difference in body mass is needed to enable grazers to coexist. Smaller herbivores should out-compete larger species through being able to survive on less food, and hence on shorter grass swards (Clutton-Brock and Harvey 1983), and accordingly displace bigger grazers from the best quality areas. The big species are able to persist elsewhere through their tolerance for less nutritious grasslands. Hence the grazing succession could be interpreted alternatively as competitive displacement governed by

body size differences (Murray and Illius 1996). Wilmshurst et al. (2000) proposed more specifically that, because of the tradeoffs between forage abundance and quality, the optimal sward biomass (and hence height) should scale allometrically with body size.

Selection for grass height is influenced additionally by the effective mouth width relative to body size, controlling the bite mass and hence rate of food ingestion achieved on grass swards differing in structure (Bell 1969 cited in Owen-Smith 1982; Gordon and Illius 1988; Owen-Smith 1989). For instance, the wide lower incisor arcade of wildebeest enables these animals to maintain a positive energy balance on shorter grass than is the case for more narrow-muzzled topi (*Damaliscus lunatus*; Murray and Brown 1993; Murray and Illius 1996). The two largest grazers among hindgut fermenters, hippo (*Hippopotamus amphibius*) and white rhino (*Ceratotherium simum*), pluck grass with their lips, and furthermore have exceptionally wide mouths enabling them to achieve an adequate food intake rate from the nutritious grazing lawns that they promote (Olivier and Laurie 1974; Owen-Smith 1988; Shrader and Owen-Smith 2006). Their reduced mass-specific metabolic requirements, coupled with longer digestive retention than smaller non-ruminants (Illius and Gordon 1992; but see Clauss and Hummel 2005), allows them also to switch to taller more fibrous grass when necessary (Owen-Smith 1988).

Studies addressing resource partitioning among grazing herbivores have been undertaken mainly in East African ecosystems where a diverse assemblage of grazing ruminants is prevalent. Our investigation was undertaken in the Hluhluwe-iMfolozi Park (HiP) in South Africa, which has a large herbivore biomass and diversity approaching that of the Serengeti ecosystem, but with white rhino the dominant species (Owen-Smith 1988). We were interested in the extent to which white rhinos, with their capacity to graze both short and tall grass, either competed with or facilitated other grazers. Our observations were focussed on the dry season when we expected competition to be accentuated as grass height became progressively reduced through grazing. We compared the grass height selected for grazing by white rhino (adult body mass 1600-2300 kg) with that chosen by three other ungulate species: zebra, a medium-large non-ruminant (adult body mass 280-340 kg); wildebeest, a medium-large and relatively wide-muzzled ruminant (adult body mass 200-280 kg); and impala (*Aepyceros melampus*), a medium-

small and relatively narrow-muzzled ruminant (adult body mass 45-70 kg). While the first three species are strict grazers, impala are mixed feeders but favour grass.

If the grass height selected depended solely on body size, the pattern of grass height partitioning depicted in Fig. 1a would be expected. However, taking into account the additional influence of relative mouth width, we considered it more likely that the pattern shown in Fig. 1b would be observed. Accordingly we expected to find (1) white rhino overlapping broadly with the other three grazers due to their acceptance of both short and tall grass, and (2) wildebeest grazing grass almost as short as that eaten by the somewhat smaller impala.

Study Area

The study was centred on the Mbuzane ranger station in the western iMfolozi section of Hluhluwe-iMfolozi Park, KwaZulu-Natal, South Africa (28° 20' S, 31° 51' E). The rainfall pattern is characterized by a wet summer from October to March, followed by a dry winter from April to September. Observations on grass height use spanned the dry season months from March to August in 1999, and from May to August in 2000. Rainfall was below average (545 mm) during the first seasonal cycle (October 1998 – September 1999), and above average (791 mm) during the second year (October 1999 – September 2000), relative to the 690 mm long term mean (1981-1998) for western HiP (KwaZulu-Natal Wildlife authority unpublished data).

White rhino (biomass 32.7 kg/ha), wildebeest (8.9 kg/ha), zebra (9.4 kg/ha) and impala (16.3 kg/ha) were the most common ungulates in the study area dependent to a greater or lesser extent on short grass. Buffalo (22.8 kg/ha) were also abundant in the park, but graze mainly taller grass, and were encountered infrequently the study region. Waterbuck (1.65 kg/ha) and warthog (2.65 kg/ha) were less common.

Methods

Observations were conducted driving a road transect of 49 km, once early in the morning and once in the late afternoon during the main feeding periods of the animals. When an

animal or herd was observed feeding within 200 meters of the road, the first animal seen grazing was chosen as the focal animal. Its feeding location was identified using nearby landmarks (trees, bushes, rocks, etc). The herd was then displaced and a $1m^2$ quadrat placed over the grass patch where feeding by this animal had occurred.

Feeding observations amounted to 20-30 records per species per month, leading to the following total sample sizes: white rhino – 215; zebra – 245; wildebeest – 246; impala – 117. Observations on impala were discontinued in 2000 in order to concentrate data collection on the remaining three species. For analysis, the earlier (March-May) and later (June-August) periods of the 1999 dry season were distinguished. In 2000, conditions remained as green through August as they had been around May 1999, hence no seasonal subdivision was made.

Each grass species present within the $1m^2$ quadrat was identified and recorded. Based on the predominant species, feeding patches were assigned to four grassland types, following Downing (1972) and Owen-Smith (1973). Grazing lawns were characterised by short or stoloniferous grass species, including *Urochloa mosambicensis, Panicum coloratum, Digitaria argyograpta, Sporobolus nitens* and *Cynodon dactylon*. *Themeda* grasslands consisted mainly of the medium-tall bunch grasses *Themeda triandra, Cymbopogon plurinodis* and *Heteropogon contortus*. Woodland or shade grasslands comprised mainly relatively tall *Panicum maximum, Panicum deustum* and *Enteropogon monostachyus*. An "other" grassland category included mostly *Bothriochloa insculpta, Eragrostis spp., Cenchrus ciliaris* and *Setaria spp.* For this paper, grazing lawns will be distinguished from a combined category of medium-tall grasslands, encompassing *Themeda*, woodland and other grassland types.

Within each sample quadrat, the leaf canopy height of the predominant grass species was estimated using a ruler. When there was a large difference between grass heights in the quadrat, the different height layers were averaged. If the grass species had been recently grazed, its pre-grazed height within the quadrat was estimated from ungrazed tillers or a nearby ungrazed tuft. For analysis, measured grass height were placed into four categories, <6 cm, 6-10 cm, 11-20 cm and ≥ 21 cm.

Data Analysis

Log linear analysis was undertaken using Statistica 2000 to examine distinctions among the three or four herbivore species in their relative use of (1) grass height (four categories), (2) grassland type (two categories) and (3) grass height within each of the two grassland type categories. Period (three seasonal distinctions) was considered as an additional factor. To test for a significant influence ($p < 0.05$), two models were compared, one incorporating the interaction and one with this interaction omitted, starting with the saturated three-way model (e.g. herbivore x height x period).

As a descriptive measure of the extent of overlap in height use between species pairs, Pianka's (1973) index was calculated: $O_{jk} = O_{kj} = \sum P_{ij} \times P_{ik} / \sqrt{\sum P_{ij}^2 \times \sum P_{ik}^2}$, where O_{jk} and O_{kj} = degree of overlap between species *j* and *k*, and P_{ij} and P_{ik} = proportions of resource *i* used by species *j* and *k* species respectively.

Results

Grass Height Use

The three-way interaction of grass height with herbivore species and period did not have a significant influence ($\chi^2 = 18.70$, df = 18, $p = 0.410$). While grass height grazed differed significantly among the herbivore species ($\chi^2 = 113.19$, df = 27, $p = 0.001$), the height of grass grazed did not differ between the periods ($\chi^2 = 29.46$, df = 24, $p = 0.203$). Hence grass height use can be compared among the herbivores independent of period within the dry season. Greatest proportional use of grass shorter than 5 cm was shown by white rhino (>0.5 of records), and least use of this height class by zebra (Figure 2). Correspondingly, zebra made relatively the most use of grass taller than 20 cm, and white rhino the least.

In pair-wise comparisons, white rhino grazed significantly different grass heights than zebra ($\chi 2 = 87.33$, df = 3, $p < 0.001$), wildebeest ($\chi^2 = 20.10$, df = 3, $p < 0.001$) and impala ($\chi^2 = 32.71$, df = 3, $p < 0.001$). The grass heights grazed by wildebeest and zebra also differed significantly ($\chi^2 = 29.36$, df = 3, $p < 0.001$). Although zebra appeared to favour less short grass and more tall grass than impala, this difference was not significant ($\chi^2 = 4.75$, df = 3, $p = 0.191$). Both showed a modal grass height grazed of 11-20 cm.

Calculations of overlap indices likewise indicated that zebra and impala were most similar in grass height grazed, while wildebeest overlapped strongly with the other three grazers (Table 1). Overlap was least between the two non-ruminants, white rhino and zebra.

Use of Grassland Categories

The three-way interaction between grassland category, herbivore species and period was not significant ($\chi^2 = 10.34$, df = 6, $p = 0.111$). However, the grassland category grazed did differ between periods ($\chi^2 = 108.59$, df = 24, $p < 0.001$), as well as between herbivore species ($\chi^2 = 76.29$, df = 27, $p < 0.001$) (Figure 3). All herbivore species except impala tended to graze less in grazing lawns during the later part of the 1999 dry season than during the earlier period, although when considered individually the difference was significant only for wildebeest ($\chi^2 = 11.63$, df = 1, $p < 0.001$). In addition, white rhino, zebra and wildebeest appeared to use grazing lawns more during the dry season of 2000 than in 1999.

In early dry 1999, zebra used grazing lawns significantly less than wildebeest ($\chi^2 = 7.75$, df = 1, $p < 0.005$), but during the later part of this dry season wildebeest made rather more use of medium-tall grassland and appeared similar to zebra (Figure 3). The apparently greater use of grazing lawns by white rhino compared with zebra was significant during early dry 1999 ($\chi^2 = 7.98$, df = 1, $p < 0.005$). White rhino and impala, and during the early dry season also wildebeest, appeared similar in their fairly even use of both lawns and taller grassland in 1999. Zebra made relatively greater use of grazing lawns in 2000 than in 1999 ($\chi^2 = 23.81$, df = 1, $p< 0.001$), but still grazed medium-tall grasslands more frequently than white rhino ($\chi^2 = 0.458$, df = 1, $p < 0.002$).

Grass Height Use Within Grassland Categories

Grass height grazed differed significantly among the herbivore species both when feeding in short grass lawns ($\chi^2 = 38.06$, df = 9, $p < 0.001$) and in medium-tall grasslands ($\chi^2 = 35.60$, df = 9, $p < 0.001$) (Figure 4). In grazing lawns, white rhino, and to a lesser extent

wildebeest and impala, concentrated on grass < 5 cm, while zebra showed an even use of height categories up to 20 cm. In medium-tall grassland, white rhino tended to neglect grass taller than 20 cm, while wildebeest and impala favoured a modal grass height of 11-20 cm, and zebra grazed grass height categories taller than 11 cm evenly.

Discussion

Contrary to expectations, the largest species, white rhino, consistently favoured shorter grass than the three smaller grazers. Moreover, the smallest species, impala, tended to favour grass heights intermediate between those grazed by wildebeest and zebra. Nevertheless, as found elsewhere, wildebeest favoured shorter swards than zebra. Hence the observed pattern of grass height use (Figure 5) was rather different from the patterns projected considering body size relationships (Figure 1). Furthermore, all species overlapped quite substantially in the grass heights that they grazed, as well as (excluding impala) in the use of grazing lawns in the dry season of the year with higher prior rainfall during the wet season.

In the Serengeti region of east Africa, wildebeest, zebra and impala favoured grass heights up to 10-25 cm during the wet season, based on crude observations from a vehicle (Sinclair 1985). In the dry season, wildebeest and impala continued to concentrate on grass heights of 10-25 cm, whereas zebra grazed grass 50-75 cm tall, a much bigger difference than we observed. In the Tarangire Park, also in east Africa, grass height post-grazing during the wet season was 3-8 cm for wildebeest compared with 9-14 cm for zebra (Voeten and Prins 1999). In the dry season, wildebeest grazed grass to 11-16 cm versus 17-30 cm for zebra, similar to our findings. In northern Botswana, zebra moved off in search of taller grass after sward height had been reduced to 20 cm (Joos-Vanderwalle 2000, reported in Owen-Smith 2002). In contrast, Serengeti wildebeest wandered in search of shorter grass once grass height exceeded 10 to 15 cm (Talbot and Talbot 1963). From detailed observations on tethered animals, Murray and Brown (1993) found that young wildebeest (body mass 86-108 kg) achieved positive energy retention once grass height exceeded 2 cm, and maximized their food intake rate on grass heights of around 5 cm (see also Wilmshurst et al. 1999).

During an earlier study conducted between 1968 and 1971 in HiP, the mean grass height grazed by white rhino increased from 10 cm in the early dry season to 24 cm by the late dry season when grass was entirely brown (Owen-Smith 1988). Associated with this was a shift from around 50% use of grazing lawns at the start of the dry season to 70-90% use of medium-tall *Themeda* grassland by August. The conditions at the time of these observations were much drier than during our later study. The prevailing density of white rhinos was also much higher during the earlier period, and probably contributed to the greater use of tall grassland. Our findings indicate that white rhinos favour grass shorter than 10 cm throughout the year if conditions permit (see also Shrader and Owen-Smith 2006).

Thomson's gazelles (body mass 25 kg) seem to obtain highest nutritional gains from grass biomass of 25 g m^{-2}, associated with a grass height of around 5 cm (Wilmshurst et al. 1999), which is little different from that reported for wildebeest. On taller swards, the food intake rate of the gazelles did not increase further, while the digestibility of the material consumed deteriorated. Extending these findings, Wilmshurst et al (2000) projected an allometric increase in the optimal sward biomass (and hence height) with increasing herbivore size. Similarly, Prins and Olff (1998) depicted smaller grazers as achieving their specific energy requirements from a lower vegetation biomass than larger species.

Our findings are inconsistent with the above interpretations. From a modelling exercise, Owen-Smith (1985) concluded that, while a medium-sized but relatively wide-mouthed ruminant like wildebeest should perform best on short grass swards, smaller herbivores with absolutely smaller bite dimensions should feed most effectively in relatively tall grass, by selectively plucking individual green leaves. Duncan (1972) and Murray and Illius (2000) noted how topi (body mass 110 kg) with a narrower muzzle than wildebeest can select the green leaf component from medium-height swards. Among the smallest grazers, mountain reedbuck (*Redunca fulvorufula*, body mass 25-30 kg) and oribi (*Oerebia oerebi*, body mass 13-20 kg) occur largely in tall grassland habitats and feed mainly on relatively tall grass tufts (Irby 1977; Oliver et al. 1978; Reilly et al. 1990), ingesting mostly leaf tissues (Owen-Smith and Cumming 1993). We found that impala (body mass 55 kg) occurred fairly unselectively across a range of grass heights.

Overall, our findings demonstrate that the grass height selected for grazing by large mammalian herbivores cannot be explained simply in terms of body size differences, as has been widely assumed. More important is the scaling of bite width relative to body mass and hence specific nutritional requirements (see Owen-Smith 1988, p. 90). The very wide mouth of a white rhino (bite width 20 cm, Owen-Smith 1988) enables it to concentrate even more strongly on short grass swards than wildebeest (incisor breadth 6.6-7.3 cm) and impala (incisor breadth 3.2 cm) (Murray and Illius 1996, Perez-Barberia and Gordon 2001). A scaling ratio calculated as the bite width (in cm) divided by the cube root of body mass (in kg) yields the following values: white rhino 1.7, wildebeest 1.15, zebra 0.85 and impala 0.85. We did not make an adjustment for specific metabolic rate, because the leaf:stem ratio in the ingested material declines with increasing body mass and hence bite dimensions (Owen-Smith 1988), counterbalancing the metabolic need to some extent. The scaling ratio of bite width seems most consistent with the comparative pattern of grass height selection among the four herbivore species that we observed. Zebra, with relatively inefficient non-ruminant digestion, need to obtain a higher food intake relative to their metabolic requirements than impala, and hence concentrate more on taller grass swards. However, domestic horses seem able to exploit very short grassland (modal height 0-4 cm in autumn, Menard et al. 2002), despite their hind-gut fermentation, perhaps because the C3 grasses prevalent in temperate latitudes are more nutritious than tropical C4 grasses (Owen-Smith 1982).

Hence, in explaining distinctions in grass height selected for grazing among large herbivores, the scaling of mouth width relative to body size, and hence to metabolic requirements, seems the overriding factor for species larger than impala. Digestive system may be an additional influence, depending on the nutritional quality of the grasses on offer. From impala size downwards, the absolute bite dimension allows animals to selectively pluck individual green leaves from grass swards of varying height, so that body size has little further effect. Hence grazing successions governed by body size differences as described for the Serengeti region may not be a widespread feature of herbivore assemblages. To explain resource partitioning among grazing ungulates, more attention needs to be given to features besides grass height, such as the grass species selected and habitat structure favoured.

References

Arsenault, R. and Owen-Smith, N. (2002). Facilitation vs. competition in grazing herbivore assemblages. Oikos 97:313-318

Bell, R.H.V. (1969). The use of the herb layer by grazing ungulates in the Serengeti National Park, Tanzania. PhD thesis, University of Manchester

Bell, R.H.V. (1970). The use of the herb layer by grazing ungulates in the Serengeti. In: Watson A (eds) Animal Populations in Relation to their Food Resources. Blackwell Scientific Publications, Oxford, pp 111-124

Bell, R.H.V. (1971). A grazing ecosystem in the Serengeti. Scientific American 224:86-93

Clauss, M. and Hummel, J. (2005). The digestive performance of mammalian herbivores: why big may not be that much better. Mammal Review 35:174-187

Clutton-Brock, T.H. and Harvey, P.H. (1983). The functional significance of variation in body size among mammals. Special Publications of the American Society of Mammalogists 7:632-663

Demment, M.W. and Van Soest, P.J. (1985). A nutritional explanation for body size patterns of ruminant and non ruminant herbivores. Am Nat 125:641-672

Downing, B.H. (1972). A plant ecological survey of the IMfolozi Game Reserve, Zululand. PhD thesis, University of Natal, Pietermaritzburg

Duncan, P. (1975). Topi and their food supply. PhD thesis, University of Nairobi

Duncan, P. , Foose, T.J., Gordon, I.J., Gakahu, C.G., and Lloyd, M. (1990). Comparative nutrient extraction from forages by bovids and equids: a test of the nutritional model of equid/bovid competition and coexistence. Oecologia 84: 411-418

Gordon, I.J. and Illius, A.W. (1988). Incisor arcade structure and diet selection in ruminants. Functional Ecology 2:15-22

Illius, A.W. and Gordon, I.J. (1987). The allometry of food intake in grazing ruminants. Journal of Animal Ecology 56:989-999

Illius, A.W. and Gordon, I.J. (1992). Modelling the nutritional ecology of ungulate herbivores: evolution of body size and competitive ability. Oecologia 89: 428-34

Irby, L.R. (1977). Food habits of Chandler's mountain reedbuck in a Rift valley ranch. E. Afr. Wildl. J. 15: 289-294

Jarman, P.J. (1974). The social organization of antelope in relation to their ecology. Behaviour 48:215-266

McNaughton, S.J. (1976). Serengeti migratory wildebeest: facilitation of energy flow by grazing. Science 191:92-94

Menard, C., Duncan, P., Fleurance, J., Georges, J.Y. and Lila, M. (2002). Comparative foraging and nutrition of horses and cattle in European wetlands. J App Ecology 39:120-133

Murray, M.G. and Brown, D. (1993). Niche Separation of grazing ungulates in the Serengeti: an experimental test. Journal of Animal Ecology 62:380-389

Murray, M.G. and Illius, A.W. (1996). Multi-species grazing in the Serengeti. In: Hodgson J, Illius AW (eds) The Ecology and Management of Grazing Systems. CAB International, pp. 247-272

Murray, M.G. and Illius, A.W. (2000). Vegetation modification and resource competition in ungulates. Oikos 89:501-508

Olivier, R.C.D. and Laurie, W.A. (1974). Habitat utilization bi hippopotamus in the Mara River East. Afr Wild J 12:249-272

Oliver, M.D.N., Short, N.R.M. and Hanks, J. (1978). Population ecology of oribi, grey rhebuck and mountain reedbuck in Highmoor State Forest Land, Natal. S Afr J Wild Res 8:95-105

Owen-Smith, N. (1973). The Behavioural Ecology of the White Rhinoceros. PhD thesis, University of Wisconsin

Owen-Smith, N. (1982). Factors influencing the consumption of plant products by large herbivores. In: The Ecology of Tropical Savannas. Huntley BJ, Walker BH (eds) Springer-Verlag, Berlin and Hamburg, pp. 359-404

Owen-Smith, N. (1985). Niche separation among African ungulates. In: Vrba ES (eds) Species and Speciation. Transvaal Museum Monograph No. 4, Pretoria, pp. 167-171

Owen-Smith, N. (1988). Megaherbivores: The Influence of Very Large Body Size on Ecology. Cambridge University Press, Cambridge

Owen-Smith N, (1989). Morphological factors and their consequences for resource partitioning among African savanna ungulates: a simulation modelling approach. In: Morris DW, Abramsky Z, Fox BJ, Willig MR (eds) Patterns and Structure of Mammalian Communities. Texas Tech University Press, pp. 155-165

Owen-Smith, N. (2002). Adaptive Herbivore Ecology: From Resources to Populations in Variable Environments. Cambridge University Press

Perez-Barberia, F.J. and Gordon, I.J. (2001). Relationship between oral morphology and feeding style in the Ungulata: a phylogenetically controlled evaluation. The Royal Society of London B 268:1023-1032

Prins, H.H.T. and Olff, H. (1998). Species richness of African grazer assemblages: towards a functional explanation. In: Dynamics of Tropical Communities. Newbury DM, Prins HHT, Brown ND (eds) Blackwell Science, 449-490

Reilly, B.K., Theron, G.K. and Bothma, J.P. (1990). Food preferences of oribi in the Golden Gate Highlands National Park. Koedoe 33:55-61

Sinclair, A.R.E. (1985). Does interspecific competition or predation shape the African ungulate community? J Animal Ecology 54:899-918

Talbot, L.M. and Talbot, M.H. (1963). The wildebeest in western Masailand, East Africa. Wildlife Monographs (12)

Vesey-Fitzgerald, D.F. (1960). Grazing succession among East African game animals. J Mammalogy 41:161-172

Voeten, M.M. and Prins, H.T. (1999). Resource partitioning between sympatric wild and domestic herbivores in East Africa. Oecologia 120: 287-294

Wilmshurst, J.F., Fryxell, J.M. and Bergman, C.M. (2000). The allometry of patch selection in ruminants. Proc R Soc Lond B 267:345-349

Wilmshurst, J.F., Fryxell, J.M. and Colucci, P.E. (1999). What constrains daily intake in Thomson's gazelles? - Ecology 80:2338-2347.

Figure Captions:

Figure 1a – Expected pattern of grass height use by the herbivore species studied considering only body mass differences.

Figure 1b – Expected pattern of grass height use considering relative mouth dimensions as well as body size.

Figure 2- Relative use of grass height categories by impala, wildebeest, zebra and white rhino.

Figure 3- Seasonal use of grazing lawns ("short") and medium-tall grasslands ("tall") by impala, wildebeest, zebra and white rhino.

Figure 4 - Relative use of grass height within grassland categories by impala, wildebeest, zebra and white rhino.

Figure 5 – Observed pattern of grass height use by the herbivore species studied.

Table 1: Overlap in the use of grass height categories by impala, wildebeest, zebra and white rhino, as assessed by Pianka's (1973) index

	Wildebeest	Zebra	White Rhino
Impala	0.87	0.90	0.75
Wildebeest	-	0.85	0.89
Zebra	-	-	0.68

Figure 1a

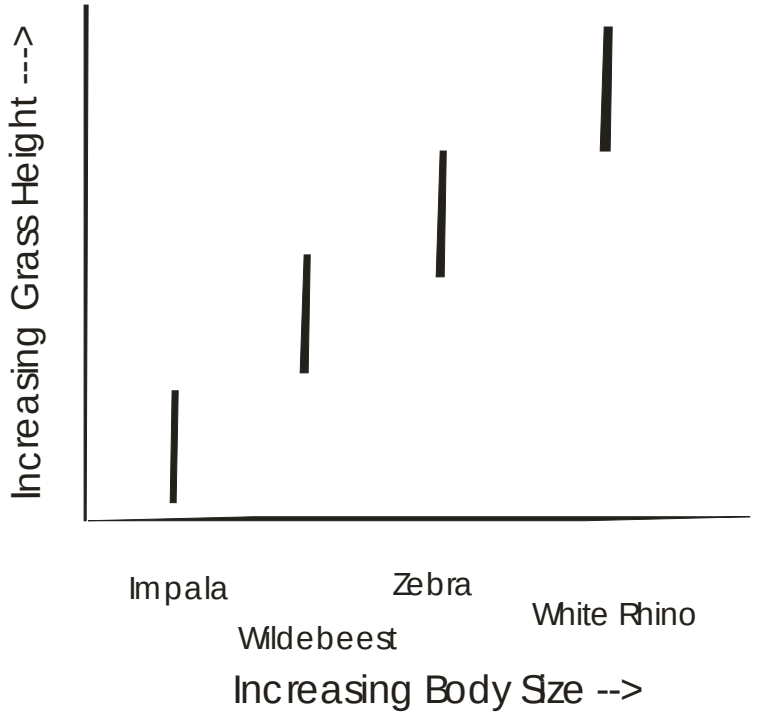


Figure 1b

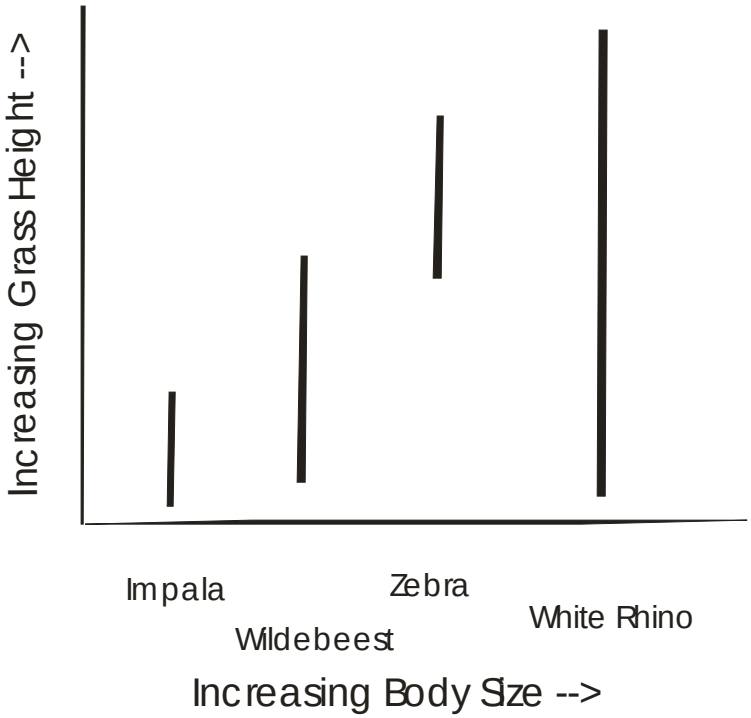


Figure 2

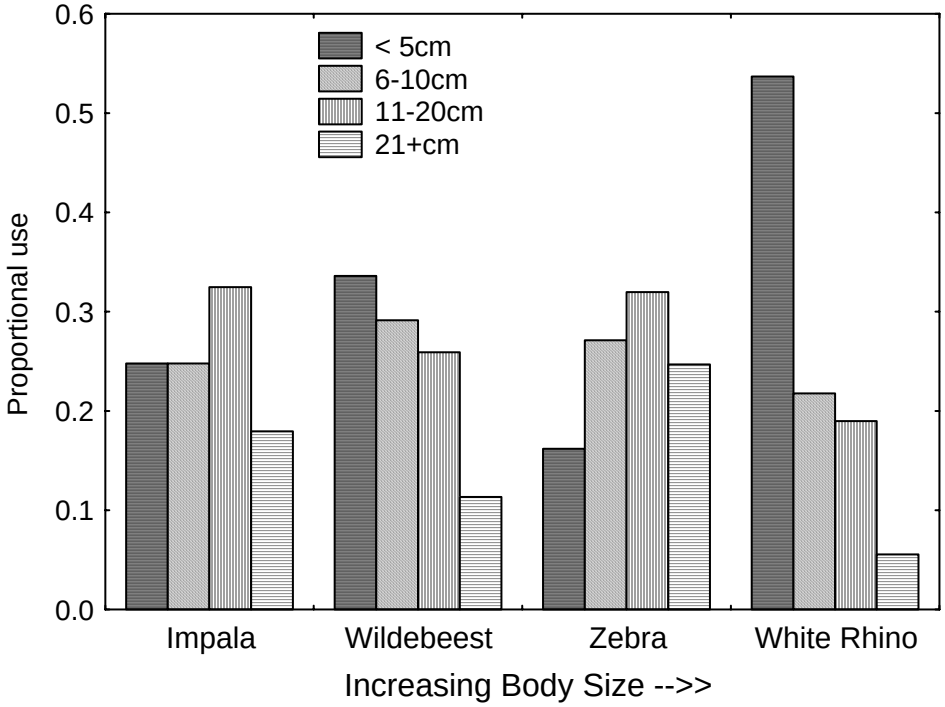


Figure 3

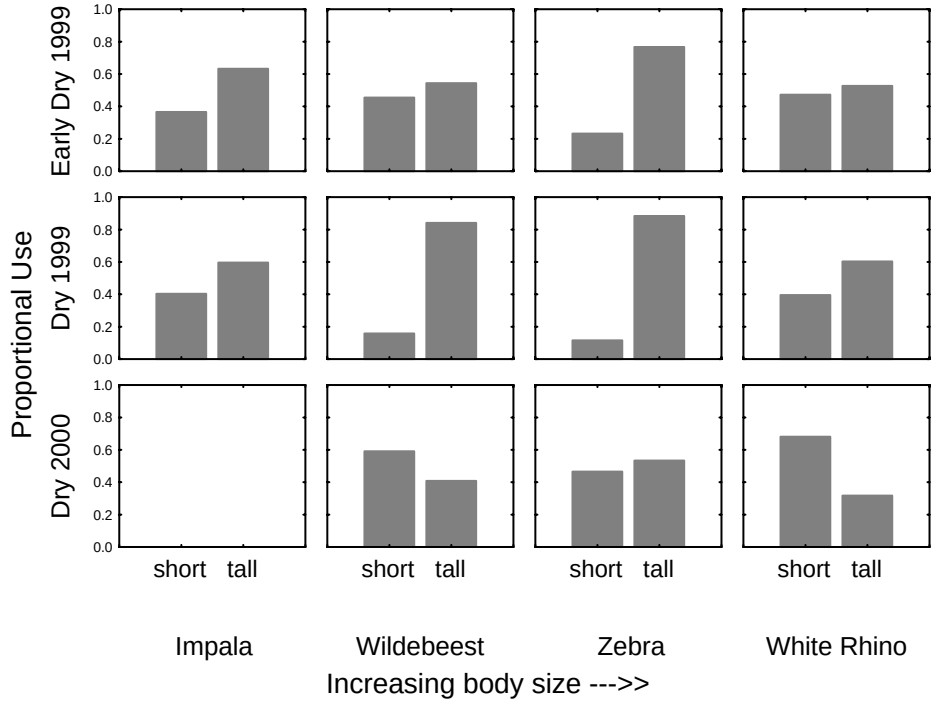


Figure 4

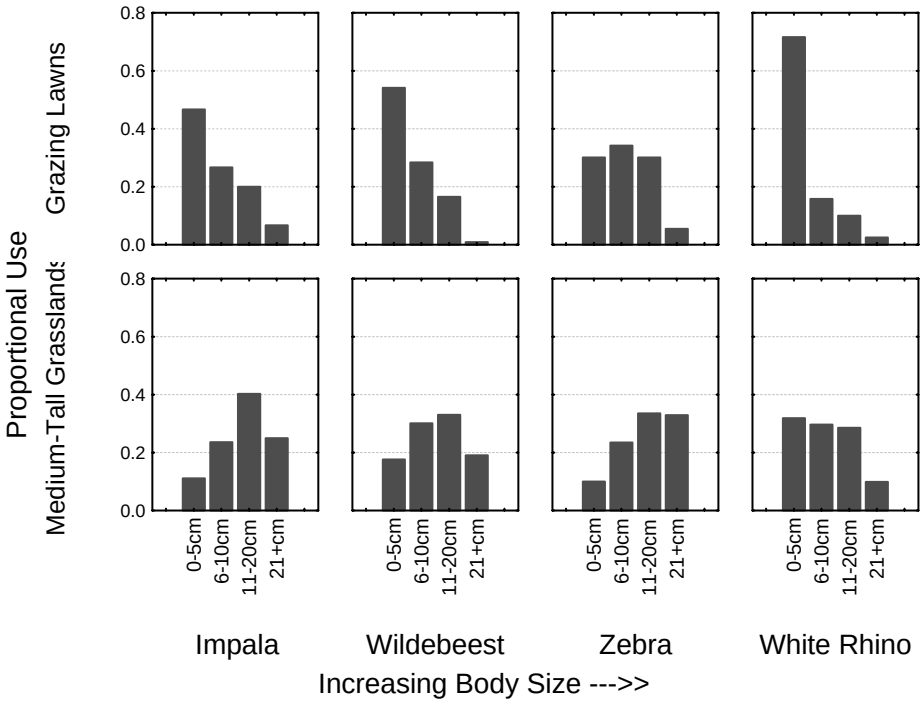
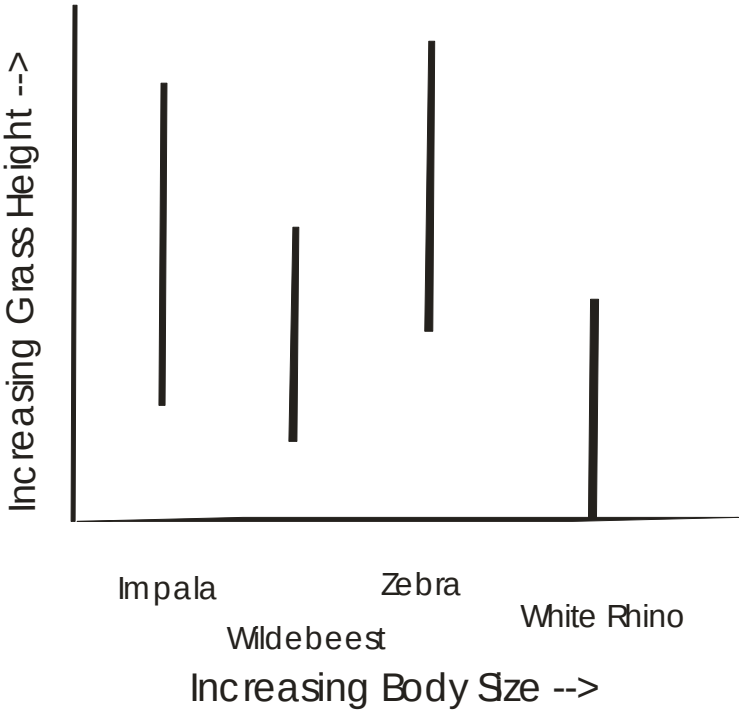


Figure 5



CHAPTER FOUR

Competition versus facilitation: the comparative use of grass resources by short grass grazers

By Randal Arsenault

Summary

I compared the dry season use of grasslands, grass species, grass height and grass greenness by white rhino and three other ungulate species, zebra, wildebeest, and impala. We were interested in the extent to which white rhinos, with their capacity to graze both short and tall grass, either competed with or facilitated other grazers. All species prefer grazing lawns during times of abundance. Zebra leave grazing lawns before other species, and wildebeest leave grazing lawns before white rhino and impala. This suggests zebra and wildebeest may be competitively excluded from grazing lawns through a reduction in grass height, by white rhino and impala, during the dry season. However, white rhino are potentially the 'supreme' facilitator increasing the availability of nutritious grazing lawns, as well as increasing the quality of those lawns through grazing in the wet season. A high dry season overlap was also found between the herbivores in Themeda, woodland and other grasslands, such that species do not appear to be partitioning these resources based on feeding patch or grass species.

Introduction

Ecologists point to Africa's species-rich communities of large mammals to illustrate the axiom that species living together must depend on different resources (Jarman and Sinclair 1979). The underlying assumption for grazing herbivores is that interspecific competition has lead to niche separation and differential preferences for grass

height and forage quality related to body size (Hutchinson 1959; Bell 1970; de Boer and Prins 1990; Murray and Illius 1996; Prins and Olff 1998). Other factors, which may also govern coexistence are predation and facilitation (McNaughton 1976; Gordon 1988; Sinclair 1985; Sinclair and Norton-Griffiths 1982). Prins and Olff (1998) suggest competition is pervasive within grazing ungulates, such that species closely similar in size rarely co-exist. The possibility exists where one species can reduce grass resources below the level that can be exploited efficiently by another species (Illius and Gordon 1987; Murray and Illius 1996; Prins and Olff 1998), and some species may benefit others by facilitating access to forage of a suitable height or quality (Vesey-Fitzgerald 1960; Bell 1970; Bell 1971; McNaughton 1976).

Food resources favoured during the early dry season are critically important in determining how long species must subsist on sub maintenance food resources later in the dry season (Owen-Smith 1989). Grazing facilitation and grazing successions have been used to describe the use of dry season resources by herbivores. In the western Serengeti, Bell (1970) studied the distribution of resident buffalo, zebra, wildebeest, topi and Thomson's gazelle across the catenary sequence of grasslands in the western Serengeti. Species concentrated on the short grassland of the upper catena until grass growth stopped and grass heights declined. Species then moved to lower ground, where medium-tall grasses occurred, in order of decreasing body size (except that topi left before the larger wildebeest). Bell (1970) argued the data suggested facilitation through a grazing succession, where smaller species later in the succession benefit from the grazing of larger species through increased leaf access in medium-tall grass stands. Although facilitation through grazing succession may have occurred in medium-tall stands, the initial movement of larger species from the upper catena was likely due to competitive exclusion through a reduction in grass height by the smaller species (Illius and Gordon 1987).

Empirical evidence on the relationship between body size and intake rate, and whether smaller species are superior competitors and better able to meet their requirements on smaller swards than larger species, is limited (Illius and Gordon 1987). Clutton-Brock and Harvey (1983) argued that larger animals cannot tolerate low sward heights that can support smaller species, and that scramble competition between species of different body sizes will lead to the exclusion of larger species from jointly preferred

swards. Arsenault and Owen-Smith (Chapter 3) suggest that the scaling of mouth width relative to body size, and hence metabolic demands, is the primary factor governing grass height selection, rather than body size alone. They showed that the mega-grazer white rhino grazed the shortest heights and the smallest species impala grazed a variety of grass heights through selective feeding for green leaf.

Habitat facilitation, where the grazing of megaherbivores transform the landscape to the benefit of others, may be another important factor promoting herbivore coexistence (Arsenault and Owen-Smith 2002),. For example, grazing Hippopotamus (*Hippopotamus amphibius*) and white rhinoceros (*Ceratotherium simum*) can transform tall grass grasslands into extensive grazing lawns (Olivier and Laurie 1974; Owen-Smith 1988). The creation and greater availability of grazing lawns, may benefit herbivores who favour grazing lawns, but be to the detriment of other species that favour taller grass. Elimination of hippos from the Mweya Peninsula region of the Queen Elizabeth National Park, Uganda, was followed by a substantial increase in elephant, buffalo and waterbuck (*Kobus ellipsiprymnus*), species favouring tall grass, after the lakeshore grassland had recovered from the short state maintained by hippo grazing (Eltringham 1974). Following the recovery of the hippo population, numbers of these three species reportedly declined in this region. The increase in white rhino abundance in the Hluhluwe-iMfolozi Park in South Africa was associated with declines by reedbuck (*Reduca arundinum*) and waterbuck, both dependent on tall grass (Owen-Smith 1988). Species preferring short grass, specifically wildebeest, zebra, impala and warthog (*Phacochoerus aethiopicus*) have maintained or increased their abundance (Arsenault and Owen-Smith 2002).

The mega-fauna today represents a small fraction of the large and diverse mega-fauna that inhabited the earth from Quaternary period to the Pleistocene epoch. It has been argued that the extinction of the Pleistocene mega-fauna could account for large changes in ecosystem structure, e.g. from open grassy to more closed wooded communities in the Holocene (Owen-Smith 1987, 1989), and that these habitat changes may have accounted for the concurrent extinction of other smaller bodied mammals.

Very few studies have compared multi-species resource use in grazing assemblages in the wild (Vesey-Fitzgerald 1960; Lamprey 1963; Bell 1970; Sinclair 1985; Putman 1996). The majority of our understanding of this complex grazing community

comes from a few multi-species studies conducted in the Serengeti (Gwynne and Ball 1969; Bell 1970; Sinclair 1985), combined with comparisons with the relatively few single species studies. Our investigation was undertaken in the Hluhluwe-iMfolozi Park (HiP) in South Africa. HiP has a large herbivore biomass and diversity approaching that of the Serengeti ecosystem, but with the megaherbivore, white rhino, the dominant species (Owen-Smith 1988). The presence of a megaherbivore may mean that the grazing guild in HiP is more similar to extinct grazing guilds.

I was interested in the extent to which white rhinos, with their capacity to graze both short and tall grass, either competed with or facilitated other grazers. My observations were focussed on the dry season when we expected competition to be accentuated as grass resources became progressively depleted. I compared the use of grasslands, grass species, grass height and grass greenness by white rhino (adult body mass 1600-2300 kg) and three other ungulate species: zebra, a medium-large non-ruminant (adult body mass 280-340 kg); wildebeest, a medium-large and relatively wide-muzzled ruminant (adult body mass 200-280 kg); and impala (*Aepyceros melampus*), a medium-small and relatively narrow-muzzled ruminant (adult body mass 45-70 kg).

I make the assumption, that in the wet season all herbivores select for high quality grazing lawns during times of abundance and when grass is not limited. I also suggest that the movement from grazing lawns to medium-tall grasslands is analogous to the movement of species down the catena, as observed in the Serengeti. When the rain stops and grass stops growing, grazing lawns are depleted and grass greenness decreases in all swards. The predicted effects on overlap in grazing lawns, medium-tall grasslands, grass height and grass greenness *as the dry season advances* are summarized in Table 1.

Hypothesis 1 – Resource Partitioning: Interspecific competition in the past has lead herbivores to partition resources, such that we predict, a) the overlap in grazing lawns will decrease, where smaller herbivores (e.g. impala) and wider mouthed herbivores (e.g. white rhino, wildebeest), graze lawns longer than non-ruminants (e.g. zebra) and larger herbivores, b) overlap in medium-tall grasslands will decrease, where smaller ruminant herbivores (e.g. impala and wildebeest), select the most nutritious grasslands and grass species, and the non-ruminants and larger species (e.g. zebra and white rhino) graze less nutritious grass, c) the overlap in grass height will decrease where larger herbivores and

non-ruminant herbivores (e.g. white rhino and zebra) graze taller grass heights than smaller ruminant herbivores (e.g. impala and wildebeest), and d) the overlap in grass greenness will decrease where the smaller ruminant herbivores (e.g. impala and wildebeest) graze greener grass than larger herbivores and non-ruminant herbivores (e.g. white rhino and zebra).

Hypothesis 2 – Competitive Exclusion: Interspecific competition through competitive exclusion predicts, a) the overlap in grazing lawns will decrease, where white rhino, wildebeest and impala graze lawns longer than zebra, b) overlap in medium-tall grasslands will decrease, where smaller ruminants (e.g. impala) and narrow mouthed herbivores selectively decrease the amount of green leaf in swards, excluding wider mouthed herbivores (e.g. white rhino and wildebeest), and bulk grazing non-ruminants (e.g. zebra), c) the overlap in grass height will decrease where larger herbivores and non-ruminant herbivores (e.g. zebra) are unable to graze short grass heights, compared to smaller and wide mouthed herbivores (e.g. impala, white rhino and wildebeest), and d) the overlap in grass greenness will decrease where the smaller and narrow mouthed grazers (e.g. impala) select more for green leaf compared to wider mouthed herbivores (e.g. white rhino and wildebeest) and non-ruminants (e.g. zebra).

Hypothesis 3 – Grazing successions as suggested by Bell (1970) predicts, a) overlap in grazing lawns decrease as body size increases, b) overlap in medium-tall grasslands and grass species will increase as smaller herbivores graze in patches previously grazed by larger herbivores, c) overlap in grass height will decrease as smaller herbivores graze in patches previously grazed by larger herbivores, and d) overlap in grass greenness will decrease as smaller herbivores graze patches with a higher percentage of green leaf, due to previous grazing of larger herbivores.

Study area

The study was centred on the Mbuzane ranger station in the western iMfolozi section of Hluhluwe-iMfolozi Park, KwaZulu-Natal, South Africa (28° 20’ S, 31° 51’ E). The rainfall pattern is characterized by a wet summer from October to March, followed by a dry winter from April to September. Observations on grass height use spanned the dry

season months from March to August in 1999, and from May to August in 2000. Rainfall was below average (545 mm) during the first seasonal cycle (October 1998 – September 1999), and above average (791 mm) during the second year (October 1999 – September 2000), relative to the 690 mm long term mean (1981-1998) for western HiP (KwaZulu-Natal Wildlife authority unpublished data).

White rhino (biomass 32.7 kg/ha), wildebeest (8.9 kg/ha), zebra (9.4 kg/ha) and impala (16.3 kg/ha) were the most common ungulates in the study area dependent to a greater or lesser extent on short grass. Buffalo (22.8 kg/ha) were also abundant in the park, but graze mainly taller grass, and were encountered infrequently the study region. Waterbuck (1.65 kg/ha) and warthog (2.65 kg/ha) were less common.

Methods

Observations were conducted driving a road transect of 49 km, once early in the morning and once in the late afternoon during the main feeding periods of the animals. When an animal or herd was observed feeding within 200 meters of the road, the first animal seen grazing was chosen as the focal animal. Its feeding location was identified using nearby landmarks (trees, bushes, rocks, etc). The herd was then displaced and a $1m^2$ quadrat placed over the grass patch where feeding by this animal had occurred.

Feeding observations amounted to 20-30 records per species per month, leading to the following total sample sizes: white rhino – 215; zebra – 245; wildebeest – 246; impala – 117. Observations on impala were discontinued in 2000 in order to concentrate data collection on the remaining three species.

Each grass species present within the $1m^2$ quadrat was identified and recorded. Based on the predominant species, feeding patches were assigned to four grassland types, following Downing (1972) and Owen-Smith (1973). Grazing lawns were characterised by short or stoloniferous grass species, including *Urochloa mosambicensis* (U.m), *Panicum coloratum* (P.col), *Digitaria argyograpta* (D.arg), *Sporobolus nitens* (Sp.n) and *Cynodon dactylon*. Themeda grasslands consisted mainly of the medium-tall bunch grasses *Themeda triandra* (Th.tr), *Cymbopogon plurinodis* and *Heteropogon contortus*. Woodland or shade grasslands comprised mainly relatively tall *Panicum maximum* (P.max), *P.*

deustum and *Enteropogon monostachyus*. An "other" grassland category included mostly *Bothriochloa insculpta* (Both), *Eragrostis superba* (E.sup), *other Eragrostis spp.*, *Cenchrus ciliaris* and *Setaria spp.* For this paper, grazing lawns will be distinguished from a combined category of medium-tall grasslands, encompassing *Themeda*, woodland and other grassland types.

Within each sample quadrat, the leaf canopy height of the predominant grass species was estimated using a ruler. When there was a large difference between grass heights in the quadrat, the different height layers were averaged. If the grass species had been recently grazed, its pre-grazed height within the quadrat was estimated from ungrazed tillers or a nearby ungrazed tuft. For analysis, measured grass height were placed into four categories, <6 cm, 6-10 cm, 11-20 cm and ≥21 cm.

The percentage of green grass compared to brown grass (all grass parts, stem, culm, leaves, etc), in the quadrat, was estimated using the 8 point scale described by Anderson and Walker (1974). The scale is as follows: Rating - 0, 1, 2, 3, 4, 5, 6, 7 corresponds to the class interval (%) - 0, 0-10, 11-25, 26-50, 51-75, 76-90, 91-99, 100, respectively. To arrive at a rating value the first question asked was: is the percentage of green within the quadrat from the ground to the top of the sward more or less than half? If the sward is more than half green, the question asked is: whether the sward is more than or less than 3/4 green. These questions continue until a rating is determined (Anderson and Walker 1974; Walker 1976). Grass greenness was then divided into four categories of green (76-100%), mainly green (50-75%), mainly brown (25-49%) and brown (0-24%).

Utilization (Ui) of grass species was calculated as: $U_i = O_i / t_m$, where O_i was the number of times herbivores were recorded eating the i^{th} grass species and t_m was the total number times a herbivore was recorded eating all grass species. The acceptance frequency ($_{Ai}$) for each grass species was determined as: $A_i = e_i / p_i$, where ei was the number of quadrats in which the ith grass species was eaten, and pi is the total number of quadrats in which the ith grass species was present (Owen-Smith and Cooper 1987).

The percentage area of the four grassland types along the drive transect was recorded by pacing 200 steps (approximately 200 m) perpendicular to the road at every 2 km, and counting the number of paces that each grassland type occupied. The percentage

of grassland types is as follows: grazing lawns (28%), *Themeda* grassland (41%), woodland grassland (16%), and other grasslands (5%).

The approximate monthly changes in grass height and grass greenness available at the foraging area and feeding patch scale were taken from my feeding observation data. The height and greenness of grasslands in foraging areas and feeding patches were averaged from all herbivore observations, for each 2 month period.

Data Analysis

Due to limited sample sizes, monthly observations were combined into 2 month periods from the start of the dry season until the end, i.e. March-April 99, May-June 99, July-August 99, as well as May-June 2000 and July-August 2000. The combined months were similar in rainfall (Figure 1). Log linear analysis was undertaken using Statistica 2000 to examine distinctions among the three or four herbivore species in their relative use of (1) grassland type (four categories) in foraging areas, (2) grassland type (four categories) in feeding patches, (3) grass height (four categories) grazed within feeding patches, and (4) grass greenness (four categories) of feeding patches. Period (5 divisions) was included as an additional factor. To test for a significant influence ($p < 0.05$), two models were compared, one incorporating the interaction and one with this interaction omitted, starting with the saturated three-way model (e.g. herbivore X grassland X period). If removing an interaction made a significant difference, standardized residuals (SR) were obtained to establish which particular cell in the contingency table had contributed mainly to this outcome (following Quinn and Keough 2002). SR values resemble z-scores, hence values less than or greater than 2 can be interpreted as indicating observed frequencies significantly different from the null expectation. Pair wise comparisons within the periods were also made between the herbivores. Letters in the figures denote the lack of statistical significance in the distributions.

As a descriptive measure of the extent of overlap in height use between species pairs, Pianka's (1973) index was also calculated: $O_{jk} = O_{kj} = \sum P_{ij} \times P_{ik} / \sqrt{\sum P_{ij}^2 \times \sum P_{ik}^2}$, where O_{jk} and O_{kj} = degree of overlap between species *j* and *k*, and P_{ij} and P_{ik} = proportions of resource *i* used by species *j* and *k* species respectively.

Correspondence analysis (CA) in Statistica (2000) was also used to depict the associations of the herbivores and resource variables.

RESULTS

Environmental conditions

Rainfall was above average in 2000 and below average in 1999 (Figure 1a). In 2000, the dry season (monthly rainfall < 20 mm) started in May, compared to March in 1999. The rains began in September in both years, such that the dry season of 2000 was 4 months long, compared to 6 months in 1999 (Figure 1a). At the feeding patch level, May-June 2000 was greener than March-April 1999 (Figure 1b). May-June 2000 was comparable to a late wet season, possibly due to high soil moisture keeping the grass swards very green (Figure 1b). March-April 1999 probably represents a typical early dry season, where most grass is mainly green, but swards are beginning to turn brown. July-August 2000 was intermediate in greenness between March-April 99 and May-June 99 (Figure 1b). May-June 1999 and July-August 1999 show that very little green grass was available after 3-6 months without rain. If the dry season was defined as swards decreasing from very green to very brown grass, the progression during our study would be 1) May-June 2000 (late wet period); 2) March-April 1999 (early dry), 3) July-August 2000 (early-mid dry), 4) May-June 1999 (mid-dry), and 5) July-August 1999 (late dry).

The percentage area of the grasslands types along the drive transect was as follows: grazing lawns (36%), Themeda (39%), woodland grassland (16%) and other grassland (9%). The changes in grass height in foraging areas and feeding patches, within grazing lawns, *Themeda* and woodland grasslands, is shown in Figure 2. Grass height available in foraging areas was generally taller than the grass height grazed in the feeding patches for all grassland types. There was little difference in the relative grass height grazed in 1999 and 2000.

1) Overlap in Grassland Use

The three-way interaction, between herbivore use of grassland type over the five periods, was not significant for either foraging areas ($\chi^2 = 38.66$, df = 36, p = 0.350; Figure 3), or feeding patches ($\chi^2 = 42.74$, df = 36, p = 0.204; Figure 4). Hence, the pattern of grassland use did not differ among the herbivore species across all periods. The use of grassland types differed significantly among herbivore species with respect to both foraging areas ($\chi^2 = 82.98$, df = 45, $p < 0.001$; Figure 3) and feeding patches ($\chi^2 = 90.81$, df = 45, $p < 0.001$; Figure 3). The grassland types used by the herbivores also changed between periods in both foraging areas ($\chi^2 = 113.35$, df = 48, $p < 0.001$; Figure 2), and feeding patches ($\chi^2 = 154.81$, df = 48, $p < 0.001$; Figure 4).

In the greenest year, 2000, there was no difference in the use of grassland type among white rhino, wildebeest and zebra in the foraging areas ($\chi^2 = 21.745$, df = 19, p = 0.297) (Figure 3; letters indicate pair wise comparisons where there was no significant difference in the distributions), but there tended to be a difference in grassland use at the feeding patch level ($\chi^2 = 27.88$, df = 18, p = 0.064) (Figure 4). In May-June 2000, white rhino, wildebeest and zebra concentrated primarily on grazing lawns in foraging areas and feeding patches (Figure 3 and Figure 4). In July-August 2000, at the feeding patch level, there was a significant difference in grassland use among herbivore species ($\chi^2 = 16.53$, df = 6, p = 0.011). Zebra tended to use more woodland grasslands (SR = +2.24) than other herbivores, and tended to use less grazing lawns (SR = -1.54) than white rhino (SR = +1.56) (Figure 4)

In 2000, there was no significant difference in the use of grasslands across the periods, by the herbivores in foraging areas ($\chi^2 = 11.46$, df = 9, p = 0.246) (Figure 3) and feeding patches ($\chi^2 = 7.27$; df = 9, p = 0.607) (Figure 4).

In the preceding drier year, 1999, the use of grassland types in the foraging areas differed significantly among the herbivores ($\chi^2 = 67.84$, df = 27, $p < 0.001$) (Figure 3). The main differences were found in the use of grazing lawns. When grazing lawns were removed from the model, the relative use of *Themeda*, woodland and other grassland types did not differ significantly among the herbivores in foraging areas ($\chi2 = 21.79$, df = 18, p = 0.242). Zebra tended to use grazing lawns less than expected, and this was most pronounced in March-April 99 (SR = -2.14) and May-June 99 (SR = -2.50), compared to the greater use of grazing lawns by wildebeest in March-April 1999 (SR = +1.89) and

white rhino in May-June 99 (SR = + 2.24) (Figure 3). Across the periods, there were differences in the use of grassland types in foraging areas by wildebeest (χ^2 = 17.86; df = 6; p < 0.007), white rhino (χ^2 = 35.24; df = 6, p < 0.001) and impala (χ^2 = 32.92; df = 6; p < 0.001), but not for zebra (χ^2 = 5.41; df = 6; p = 0.492). Wildebeest tended to use other grasslands less in March-April (SR = -2.16) and more in May-June 1999 (SR = +1.79). White rhino favoured Themeda in March-April 1999 (SR = +3.00) compared to other periods, and impala tended to graze woodland more than expected in July-August 1999 (SR = +2.10). Across the periods in 1999, the herbivores grazed relatively similar amounts of grazing lawns in the foraging areas (Figure 3).

At the feeding patch level in 1999, the use of grassland types likewise differed significantly among the herbivores (χ^2 = 62.94, df = 27, p < 0.001) (Figure 4). Zebra tended to use grazing lawns less than expected in March-April 99 (SR = - 1.28) compared to wildebeest (SR = +1.56), and zebra used lawns less than expected in May-June 99 (SR = -2.37) compared to white rhino (SR = +1.79) (Figure 4). In the driest period July-August 99, zebra and wildebeest tended to use grazing lawns less (SR = - 1.56, SR = - 1.51 respectively), than white rhino (SR = +1.84) and impala (SR = +1.48) (Figure 4). When grazing lawns were removed from the model, there was no significant difference in the relative use of Themeda, woodland and other grasslands by the herbivores at the feeding patch level (χ^2 = 24.45, df = 18, p = 0.141). However, in July-August 1999, wildebeest used other grass types (SR = +2.03) and *Themeda* grasslands (SR = +2.05) more than expected, compared to white rhino, wildebeest and impala (Figure 4). Wildebeest also tended to use woodland grasslands (SR = -1.40) less than expected in July-August 1999, compared to zebra (SR = +1.46) (Figure 4).

Across the periods in 1999, there were differences in the use of grassland types in feeding patches by wildebeest (χ^2 = 34.06; df = 6; p < 0.001), white rhino (χ^2 = 17.85, df = 6, p < 0.007), impala (χ^2 = 18.22; df = 6; p < 0.006), and zebra (χ^2 = 16.98, df = 6, p < 0.009) (Figure 4). Wildebeest decreased their use of grazing lawns from March-April 1999 (SR = +2.54) to July-August (SR = - 2.57), and utilized more other grasslands in May-June 1999 (SR = +2.19) compared to March-April 1999 (SR = -2.69) (Figure 4). Zebra, impala and white rhino tended to use more woodland grasslands in July-August 1999 than other periods (SR = +2.35, SR = +2.61, SR = +2.03. respectively).

Overlap in the use grassland types in 2000 was generally high in both foraging areas and feeding patches (Table 2 and Table 3). In most periods of 1999, overlap was highest between white rhino and impala, and the lowest between zebra and wildebeest (Table 2 and Table 3). Overlap was also generally high in March-April 1999 at the start of the dry season, with the exception of zebra and wildebeest. Overlap between white rhino and wildebeest showed a greater decrease in feeding patches (Table 3), compared to foraging areas (Table 2). Overlap between wildebeest and impala also decreased as the dry season advanced. The lowest overlap value was found between white rhino and zebra in May-June 1999, although overlap was relatively high in the other periods.

2) Overlap in Height Use

At the feeding patch level, there was a significant difference in the grass height grazed among the herbivores ($\chi^2 = 134.49$, df = 45, $p < 0.001$) (Figure 6; letters indicate pair wise comparisons where there was no significant difference in the distributions). The main differences were found between the use of grass below 6 cm and grass above 21+ cm. In March-April 99, white rhino (SR = + 2.27) and wildebeest (SR = + 1.97) tended to graze grass below 6 cm more than zebra (SR = - 2.37) and impala (SR = - 1.55) (Figure 6). In most other periods, white rhino tended to graze grass below 6 cm more frequently than other herbivores (Figure 5). Zebra tended to graze grass above 21 cm more than white rhino in all periods, except March-April 1999 (Figure 6).

In 1999, wildebeest grazed shorter grass heights similar to white rhino in March-April 1999 ($\chi^2 = 2.87$, df = 3, $p = 0.412$), but grazed taller grass heights than white rhino in May-June 1999 ($\chi^2 = 12.04$, df = 3, $p < 0.007$) and July-August 1999 ($\chi^2 = 12.13$, df = 3, $p < 0.007$) (Figure 6). Conversely, wildebeest grazed shorter heights compared to zebra in March-April 1999 ($\chi^2 = 20.29$, df = 3, $p < 0.000$), and tended to use taller grass heights more similar to zebra in July-August 1999 ($\chi^2 = 6.93$, df = 3, $p = 0.074$) (Figure 5). There was no significant difference in the use of grass heights by impala, wildebeest and zebra in the driest period July-August 1999 ($\chi^2 = 9.60$, df = 6, $p = 0.142$) (Figure 6).

Across the periods in 1999, there was a significant difference in the heights of grass grazed by wildebeest ($\chi^2 = 20.79$, df = 6, $p < 0.002$), zebra ($\chi^2 = 14.40$, df = 6, P <

0.025) and impala ($\chi^2 = 20.95$, df = 6, $p < 0.002$), but not white rhino ($\chi^2 = 9.62$, df = 6, p = 0.141). Wildebeest tended to graze heights above 21 cm less in March-April 1999 (SR = -2.25) and heights below 6 cm less in July-August 1999 (SR = - 1.68) (Figure 6). Zebra tended to graze heights above 21 cm less in March-April 1999 (SR = -2..15), and impala tended to graze less heights above 21 cm less in May-June 1999 (SR = -1.83).

Overlap in grass height use was the lowest between white rhino and zebra, and white rhino and impala (Table 4). Overlap in height use decreased between white rhino and wildebeest in 1999 as the dry season advanced, compared with 2000. Overlap increased between wildebeest and impala in May-June 1999, and decreased between impala and zebra in May-June 1999. Overlap in height use increased between wildebeest and zebra in 1999, but decreased in 2000, as the dry season advanced (Table 4).

3) Overlap in Grass Greenness

Within the periods, there was no significant difference between the grass greenness in feeding patches among herbivore species ($\chi^2 = 50.62$, df = 45, p = 0.262).

Overlap of all resource variables

The highest degree of overall overlap was found between the herbivores in May-June 2000, and between white rhino and wildebeest in July-August 2000 and March-April 1999 (Table 5). Zebra and impala also showed high overall overlap in March-April and July-August 1999. The lowest overall overlap was found between white rhino and zebra, especially in May-June and July-August 1999, and between wildebeest and zebra in March-April and May-June 1999. Overlap decreased between white rhino and wildebeest as the dry season advanced in 1999, and overlap tended to increase between zebra and wildebeest in 1999 (Table 5).

Utilization and acceptance of grass species

At the feeding patch scale in 1999, wildebeest and zebra decreased their use of short grass species when foraging in grazing lawns, compared with white rhino and impala (Figure 4). Therefore wildebeest and zebra were selecting feeding patches with Themeda, woodland or other grass species when found in grazing lawns in the mid and dry season of 1999, than white rhino and impala. In July-August 1999, wildebeest increased their utilization of *Themeda triandra*, *Panicum maximum* and *Eragrostis superba*, compared to a decrease in the use of short grass species (Table 4). In iMfolozi *Eragrostis superba* and *Themeda triandra* are often found interspersed throughout grazing lawns. *Panicum maximum* is found under trees occurring throughout grazing lawns. Zebra also showed increases in the use of *Eragrostis superba* in May-June 99, and a large increase in the use of *Panicum maximum* in July-August 99 compared with wildebeest (Table 4).

Overall, the herbivores seemed to favour the same grass species within each grassland type. All of the herbivores tended to graze *Panicum coloratum* or *Urochloa mosambicensis* more than other short grass species (Table 4). Utilization of short grass species was generally higher in 2000, compared to 1999 (Table 4). Acceptability for short grass species much higher in the greenest year 2000, compared to 1999 (Table 5). The utilization of short grass species by zebra and wildebeest decreased in the driest periods May-June and July-August 1999, compared to white rhino and impala (Table 4). This is similar to the pattern of grazing lawn use at the feeding patch level (Figure 3). Acceptability of short grass species also decreased for zebra and wildebeest during the dry season of 1999, compared to white rhino and impala (Table 5). The acceptability of *Panicum maximum* was relatively high for all herbivores compared to the other grass species (Table 5). The overall utilization of *Panicum maximum* was 34% for zebra and 32 % for impala, whereas white rhino utilized *Panicum maximum* 20% and wildebeest 16% (Table 4).

Correspondence Analysis

Figure 6 is the output of the correspondence analysis depicting the patterns of resource use over three periods, early dry 1999, late dry 1999 and dry 2000. I condensed the periods to reduce the number of figures while still representing the overall patterns.

The main factor contributing to separation along the x-axis was grass height, from short (1: 0-5 cm) to tall grass (4: >21 cm) (Figure 6). Grazing lawns corresponded to short grass heights, whereas *Themeda*, woodland and other grasslands corresponded to taller grass heights (Figure 5). White rhino correspond with grazing lawns and very short grass heights in all periods, and zebra associate with taller grass heights and a mix of woodland, *Themeda* and other grassland types (Figure 6). In early dry 99 and dry season 2000, wildebeest associated with grazing lawns and very short grass heights, whereas in late dry 99 wildebeest associated with intermediate grass heights in *Themeda* and other grasslands. Impala associated with intermediate grass heights and a mix of grassland types, corresponding more towards woodland in late dry 1999. In late dry 99, grazing lawns in the foraging areas (L-a) correspond more towards the centre than grazing lawns in feeding patches (L-p). This corresponds with herbivores using relatively more grazing lawns at the foraging area scale than the feeding patch scale (Figure 2 and Figure 3).

Discussion

In the greenest period May-June 2000, all herbivores observed, white rhino, zebra and wildebeest, concentrated on grazing lawns. This suggests the assumption that during times of abundance all species prefer nutritious short grass species is correct. The main difference was found in the drier year, 1999, and this was related to whether or not herbivores concentrated on shorter grass heights and consequently grazing lawns. White rhino showed the greatest preference for grazing lawns and concentrated on grass below 6 cm. Zebra used grazing lawns the least in 1999, and concentrated on taller grass heights. As the dry season of 1999 advanced, wildebeest decreased their use of grazing lawns at the feeding patch scale, compared to white rhino and impala. This decrease in grazing lawn use by wildebeest was evident at the feeding patch scale, but not at the foraging area scale.

Resource use by herbivores can be observed at a variety of scales. Herbivores selectively consume certain plant parts and species, and forage preferentially in particular vegetation types and landscape regions (Senft et al. 1987; Bailey et al. 1996). Even in uniform grass swards, herbivores create a patch structure with the first bite that they take,

depleting food in the spot where they fed relative to the surrounding matrix (Owen-Smith 2002). No multi-species studies to my knowledge have compared grassland use and grass height grazed in foraging areas and feeding patches, as well as grass species eaten. For example, Sinclair (1985) and Voeten and Prins (1999) compared the use of foraging areas, making observations from a vehicle or throwing random quadrats in foraging areas. In out study, grassland type use in foraging areas was found to be too broad in scale to detect differences found at the feeding patch level. Whereas, grass species use correlated well with grassland type use in feeding patches. For example, although wildebeest and zebra were found using grazing lawns at the foraging area scale, information at the feeding patch and grass species scale showed wildebeest and zebra grazing medium-tall grass species, while in grazing lawn foraging areas (Figure 4).

The use of grazing lawns

The seasonal decrease in use of grazing lawns by zebra and wildebeest, could be due to either resource partitioning (Hypothesis 1) or competitive exclusion (Hypothesis 2) (Table 1). Zebra are hind-gut fermenters, and have evolved the ability to digest lower quality forage, through higher intake, and higher throughput compared to ruminants (Bell 1971; Janis 1976; Duncan et al, 1990). Zebra have been shown elsewhere in Africa to graze taller heights than wildebeest in the dry season (Sinclair 1985; Voeten and Prins 1999). In the dry season in Tarangire, Tanzania, the mean grass height grazed for zebra was 25 cm, versus 14 cm for wildebeest (Voeten and Prins 1999). In the Serengeti, zebra concentrated on foraging areas up to 50 and 75 cm in the dry season, and wildebeest concentrated on foraging areas below 25 cm (Sinclair 1985). Zebra graze grass consisting of a suitable mix of quickly fermentable carbohydrates with completely indigestible fibber (Janis 1976). Quickly digestible grass parts are digested, and the remainder is passed out of the gut to make way for more food (Janis 1976). Zebra are also able to crop grasses very close to ground level like horses (Duncan 1992; Putman 1996). However, Voeten and Prins postulate that if swards are too short, zebra may not be able to fulfil their higher intake requirements (Voeten and Prins 2000). Domestic horses have been shown to exploit

very short grassland, but this may be because the C3 grasses prevalent in temperate latitudes are more nutritious than tropical C4 grasses (Owen-Smith 1982).

The movement of zebra from grazing lawns early in the dry season in iMfolozi seems consistent with the movement of zebra from the upper catenas in the Serengeti. Illius and Gordon (1987) suggested this movement from the upper catena was driven by smaller species excluding the larger species from mutually preferred swards. We found further evidence that zebra are the first species to be excluded from gazing lawns. Zebra likely shift and graze medium-tall grasslands due differences in non-ruminant digestion. Resource partitioning to use lower quality grasslands later in the dry season may be a more important factor governing populations and co-existence of zebra.

The resource partitioning hypothesis (H1) does not explain the decrease in grazing lawn use, by wildebeest, at the feeding patch level in 1999. Wildebeest have relatively broader muzzles than other ruminants, enabling higher intake rates on short grass swards compared to narrow mouthed ruminants of similar size (Hofmann 1989; Illius and Gordon 1987; Owen-Smith 1985). Murray and Brown (1993) demonstrated that wildebeest had higher intake rates and could maintain positive energy retention on shorter swards than the smaller more narrow mouthed, topi. When it is available, wildebeest eat very short green grass, and move in search of fresh re-growth when grass height exceeds 10-15 cm (Talbot and Talbot 1963).

Compared to iMfolozi, the Serengeti has a shorter dry season with periodic rains, leading to green flush (Maddock 1979). The dry season in iMfolozi, as seen in 1999, has little to no rain throughout the six month dry season. Once soil moisture was depleted, all swards, including grazing lawns were mainly brown. The decrease in grazing lawn use by wildebeest in comparison to white rhino and impala in iMfolozi was somewhat unexpected, when compared to how migratory wildebeest dominate grazing lawns in the Serengeti. However in Kruger National Park, South Africa, Ben-Shahar (1991) showed that the wildebeest grazed different grass species during the limiting season, which were not grazed during the growing season. Wildebeest in vast herds have also been reported to graze down tall *Themeda* grass in the northern section of the Serengeti ecosystem (Jarman and Sinclair 1979).

Our study is the first to document a similar pattern of grazing lawn use by zebra and wildebeest, as observed by Bell (1970) on the upper catenas in the Serengeti. As the dry season advanced, wildebeest decreased their use of grazing lawns compared to impala and white rhino, but used lawns longer than zebra. This is further evidence that the mechanism for leaving grazing lawns is competitive exclusion as grass is depleted by white rhino and possibly impala.

Smaller species, such as Thomson's gazelle in the Serengeti, theoretically have the potential to out compete larger species by depressing vegetation biomass to where larger species are unable to meet their greater absolute food requirements (Illius and Gordon 1987). Impala, in our study, used grazing lawns longer into the dry season than zebra and wildebeest. This is similar to observations of Thomson's gazelle in the Serengeti (Bell 1970). However impala tended to graze taller grass heights and less grass below 6 cm than white rhino. Impala may have been more selective for grass leaf above 5 cm. Impala are also known to prefer browse during the dry season, and grass during the wet season (Jarman and Sinclair 1979). Although we present evidence of impala using lawns during the dry season, impala were also observed browsing fallen *Acacia nigrescens* leaves in grazing lawns (pers. Obs.).

White rhino concentrated on grazing lawns and grazed grass below 6 cm more than other herbivores throughout the dry season. However during an earlier study conducted between 1968 and 1971 in HiP, the mean grass height grazed by white rhino increased from 10 cm in the early dry season to 24 cm by the late dry season when grass was entirely brown (Owen-Smith 1988). Associated with this was a shift from around 50% use of grazing lawns at the start of the dry season to 70-90% use of medium-tall *Themeda* grassland by August. The conditions at the time of these observations were much drier than during our later study. The prevailing density of white rhinos was also much higher during the earlier period, and probably contributed to the greater use of tall grassland.

Resource partitioning (H1) seems to explain white rhino use of grazing lawns. White rhino and hippos have evolved the ability to maintain sufficient intake on short swards through an increase in relative mouth width and the expansion of the lips (Owen-Smith 1988). However, compared to ruminants, evidence suggests that the passage rate of food for white rhino is relatively short (Foose 1982), and similar to other non-ruminant

species (Demment and van Soest 1985), white rhino should be able to process high fibre diets without it having a detrimental effect on intake. Our findings indicate that when conditions permit and grazing lawns are available, white rhinos favour grass shorter than 10 cm throughout the year (see also Shrader and Owen-Smith 2006).

The use of medium-tall grasslands

There was little difference in the dry season use of *Themeda*, woodland and other grasslands by white rhino, zebra and impala. There was also little difference in grass height use between wildebeest, zebra and impala in the driest period July-August 1999. Therefore there is little evidence for resource partitioning (H1) in the use of medium-tall grassland types between these species. Woodland grassland appears to be the next favoured grass type after grazing lawns for most species during the dry season. However, in the driest period, July –August 99, wildebeest use more *Themeda* and *Eragrostis superba*, and tended to use less *Panicum maximum*. It is interesting to point out that although zebra are expected to benefit more from eating a wider quality range of food types than similar size ruminants (Owen-Smith 1985; Owen-Smith 2002), zebra concentrated on *Panicum maximum* in 1999 and 2000, later in the dry season. Owaga (1973) suggested wildebeest actively select for leaf in all seasons, while zebra select for grass sheath in the dry season, feeding unselectively in the wet season. Wildebeest are expected to be more selective for grass quality due to their ruminant digestion, compared to the non-ruminant zebra. *Panicum maximum* is generally considered a higher quality grass than *Themeda*, and *Eragrostis superba*. Wildebeest would be expected to select for the "next best" grass, i.e. *Panicum maximum*, but appear to be less selective for *Panicum maximum* than zebra. Jarman (1974) described wildebeest as being rather unselective for grass species and more selective for plant parts or growth stages. Wildebeest concentrated on shorter grass heights earlier in the dry season of 1999 compared to zebra but used grass heights similarly in July-August 1999. It is possible wildebeest may be avoiding woodland grasses due to the greater risk of predation.

Bell (1970) suggested that during the dry season wildebeest maximized their intake of grass leaves by migration or association with less selective ungulates in a grazing

succession. There is little evidence, in my study, of a grazing succession in grassland types, where zebra graze a grassland type first, then wildebeest, and then impala. However, white rhino concentrated on shorter grass heights than zebra in medium-tall grasslands, and wildebeest tended to utilize shorter grass heights than zebra earlier in the dry season. This may suggest wildebeest and white rhino are selecting swards previously grazed by zebra. White rhino may benefit from grazing previously grazed swards but also have the ability through non-ruminant digestion to digest high stem swards when higher quality short swards are no longer available (Owen-Smith 1988). A wider muzzle means wildebeest may ingest a higher proportion of stem tissues from tall grass swards (Berry 1980). However, in the driest period, July-August 1999, there was little difference in grass height use between wildebeest and zebra. Although theoretically some grazers may benefit in the short term from the reduction in height by another species, there is little evidence our study, or in the literature, that grazing successions are a major mechanism influencing coexistence.

However, "habitat facilitation", where the feeding by one herbivore can affect changes in grass species composition, would affect herbivore populations (either facilitative or competitive) (Arsenault and Owen-Smith 2002). For example, white rhino and hippopotamus are known to transform tall grasslands to grazing lawns over extensive areas (Eltringham 1974; Owen-Smith 1988). Owen-Smith (1988) argued that megaherbivores are likely to be keystone herbivores because populations are food limited, rather than predator limited, and because of their large food requirements per individual. Keystone species exert disproportionately large effects on an ecosystems function and compositions relative to their number (Power et al. 1996), and it has been suggested that white rhino may play a greater role in the creation and maintenance of grazing lawns in HiP than other species of grazer (Owen-Smith 1979). Therefore the presence of white rhino may be more of a benefit to wildebeest, impala, and zebra, counteracting any negative effects of competitive exclusion.

Arsenault and Owen-Smith (2002) suggested that grazing facilitation and increased quality of grazing of lawns in the growing season may ameliorate exploitative competition that comes into operation during the dormant season, and that this is an important mechanism promoting species coexistence within grazing herbivore assemblages. All

herbivores tended to concentrate on grazing lawns during the greenest period May-June 2000, suggesting that grazing lawns were also preferred during the wet season. The benefit of white rhino creating greater availability of grazing lawns within the landscape, combined with grazing facilitation in the wet season, may out weigh any negative affects of competition in the dry season. For example, the facilitation of habitat and increased food quality may improve overall recruitment success. The overall demographic consequence depends on the balance between the temporal tradeoffs between benefits in the growing season and competition in the dormant season.

In the early dry season, grazing lawns would become quickly depleted for all herbivores. There may be little benefit to these very short grazing lawns for any species, even white rhino, during these very dry periods. Jarman and Sinclair (1979) suggested that the larger species, which benefit most by the high average quality of pasture in the wet season, can better afford a strategy of protein storage in the wet season to carry them through the poverty of the dry season. Recently, Shrader and Owen-Smith (in press) suggested white rhino may be grazing on lawns in the mid-late dry season in order to avoid tall stemy grasses, and using protein reserves while waiting for the next rain. In addition, impala may be selecting for *Acacia nigrescens* and other browse in grazing lawns.

Conclusions

Although evidence suggests that zebra and wildebeest are excluded from grazing lawns in the dry season, whether this negatively affects their populations is unknown. The benefit of a greater availability of grazing lawns due to white rhino grazing, and facilitation through increased quality in the growing season, may out weigh any negative affects of competition during the dry season. The differences found in the use of grass height and grassland use is mainly explained by the ability of some grazers to graze short heights and grazing lawns as the dry season advances. This is best explained by the scaling of mouth width relative to body size, rather than body size alone (Chapter 3). However, grazing lawns may be depleted quickly in the dry season and little benefit to all herbivores, such that white rhino may be surviving on protein reserves and impala shifting

to browse. Zebra have the ability to graze lower quality medium-tall grass resources and taller heights through a faster throughput and hindgut digestion. Whereas, wildebeest may be most negatively affected by competition for grazing lawns, although this may only affect populations in times of extremes, such as drought years. Finally, the dry season overlap in medium-tall grasslands between zebra, wildebeest, white rhino and impala was found to be generally high. Therefore there is little evidence from our research that herbivores partitioning resources during the dry season or that smaller species benefit from grazing successions.

REFERENCES

Arsenault, R. and Owen-Smith, N. (2002). Facilitation vs. competition in grazing herbivore assemblages. Oikos 97:313-318.

Bailey, D. W., Gross, J. E., Laca, E. A., Rittenhouse, L. R., Coughenour, M. B., Swift, D. M., and Sims, P. L. (1996). Mechanisms that result in large herbivore grazing patterns. Journal of Range Management 49(5), 386-400.

Bell, R. H. V. (1970). The use of the herb layer by grazing ungulates in the Serengeti. Animal Populations in Relation to their Food Resources, A. Watson, ed., Blackwell Scientific Publications, Oxford, 111-124.

Bell, R. H. V. (1971). A grazing ecosystem in the Serengeti. Scientific American 224, 86-93.

Ben-Shahar, R (1991). Selectivity in large generalist herbivores: feeding patterns of African ungulates in a semi-arid habitat. African Journal of Ecology 29: 302-315.

Berry, H.H. (1980). Behavioural and ecophysiological studies on the blue wildebeest at the Etosha National Park. Ph.D Thesis. University of Cape Town.

Clutton-Brock, T. H. and Harvey, P. H. (1983). The functional significance of variation in body size among mammals. - Special Publications of the American Society of Mammalogists 7:632-663.

de Boer, W. F., and Prins, H. H. T. (1990). Large herbivores that strive mightily but eat and drink as friends. Oecologia, 82, 264-274.

Duncan, P. (1992). Horses and grasses: the nutritional ecology of equids and their impact on the Camargue (Ecological studies 87). Springer, Berlin, Heidelberg, New York.

Duncan, P., Foose, T. J., Gordon, I. J., Gakahu, C. G. and Lloyd, M. (1990). Comparative nutrient extraction from forages by bovids and equids: a test of the nutritional model of equid/bovid competition and coexistence. Oecologia 84: 411-418.

Eltringham, S. K. (1974). Changes in the large mammal community of Mweya Peninsula, Rwenzori National Park, Uganda, following removal of Hippopotamus. - Journal of Applied Ecology 11:855-865.

Foose, T. (1982). Trophic strategies of ruminant versus non-ruminant ungulates. PhD dissertation, University of Chicago, Chicago

Gordon, I. J. (1988). Facilitation of red deer grazing by cattle and its impact on red deer performance. Journal of Applied Ecology, 25, 1-10.

Gwynne, M. D., and Bell, R. H. V. (1968). Selection of vegetation components by grazing ungulates in the Serengeti National Park. Nature 220, 390-393.

Hofmann, R. R. (1989). Evolutionary steps of ecophysiological adaptation and diversification of ruminants: A comparative review of their digestive system. Oecologia 78: 443-457.

Hutchinson, G. E. (1959). Homage to Santa Rosalie, or why are there so many kinds of animals? Am. Nat. 93: 145-159.

Illius, A. W., and Gordon, I. J. (1987). The allometry of food intake in grazing ruminants. Journal of Animal Ecology, 56, 989-999.

Jarman, P. J. (1974). The social organization of antelope in relation to their ecology. Behaviour, 48, 215-266.

Jarman, P. J., and Sinclair, A. R. E. (1979). Feeding strategy and the pattern of resource partitioning in ungulates. In: Serengeti: Dynamics of an Ecosystem, A. R. E. Sinclair and M. Norton-Griffiths, eds., University of Chicago Press, Chicago.

Janis, C. (1976). The evolutionary strategy of the Equidae and the origins of rumen and cecal digestion. Evolution 30: 757-776.

Lamprey, H. F. (1963). Ecological separation of the large mammal species in Tarangire Game Reserve, Tanzania. East African Wildlife Journal 1: 63-92.

MacArthur, R. H. (1972). Geographical Ecology, Harper and Row, New York.

Maddock, L. (1979). The “Migration” and Grazing Succession. In: Serengeti: Dynamics of an Ecosystem, A. R. E. Sinclair and M. Norton-Griffiths, eds., University of Chicago Press, Chicago.

McNaughton, S. J. (1976). Serengeti migratory wildebeest: facilitation of energy flow by grazing. Science 191, 92-94.

Murray, M. G., and Brown, D. (1993). Niche Separation of grazing ungulates in the Serengeti: an experimental test. Journal of Animal Ecology 62, 380-389.

Murray, M. G., and Illius, A. W. (1996). Multi-species grazing in the Serengeti. The Ecology and Management of Grazing Systems, J. Hodgson and A. W. Illius, eds., CAB International, 247-272.

Murray, M. G. and Illius, A. W. (2000). Vegetation modification and resource competition in ungulates. – Oikos 89: 501-508.

Olivier, R.C.D. and W.A. Laurie (1974). Habitat utilization bi hippopotamus in the Mara River East. African Wildlife Journal. 12: 249-272.

Owaga, M.L. (1975). The feeding ecology of wildebeest and zebra in the Anthi-Kaputei plains. East African Wildlife Journal. 13: 375-383.

Owen-Smith, N. (1985). Niche separation among African ungulates. Species and Speciation, E. S. Vrba, ed., Transvaal Museum Monograph No. 4, Pretoria, 167-171.

Owen-Smith, N. (1987). The Pleistocene extinctions: the pivotal role of megaherbivores. Paliobiology 13: 351-362

Owen-Smith, N. (1988). Megaherbivores: The influence of very large body size on ecology, Cambridge University Press, Cambridge.

Owen-Smith, N. (1989). Morphological factors and their consequences for resource partitioning among African savanna ungulates: a simulation modelling approach. Patterns and Structure of Mammalian Communities, D. W. Morris, Z. Abramsky, B. J. Fox, and M. R. Willig, eds., Texas Tech University Press, 155-165.

Owen-Smith, N. 2002. Adaptive Herbivore Ecology: From Resources to Populations in Variable Environments. Cambridge University Press.

Owen-Smith, N., and Novellie, P. (1982). What should a clever ungulate eat? American Naturalist, 119(2), 151-177.

Quinn G.P. and J. Keough 2002. Experimental design and data analysis for biologists. Cambridge University Press.

Power, M.E, Tilman, D., Estes, J.A., Menge, B.A, Bond, W., Mills, L.S, Daily, G,. Castilla, J. C., Lubchenco, J and Paine, R. T. (1996). Challenges in the quest for keystones. Bioscience 46(8): 609-620.

Perez-Barberia, F.J., and Gordon, I.J. (2001). Relationship between oral morphology and feeding style in the Ungulata: a phylogenetically controlled evaluation. The Royal Society of London B. 268: 1023-1032

Prins, H. H. T., and Olff, H. (1996). Species richness of African grazer assemblages: towards a functional explanation. Dynamics of Tropical Communities, D. M. Newbury, H. H. T. Prins, and N. D. Brown, eds., Blackwell Science, 449-490.

Putman, R. J. (1996). Competition and Resource Partitioning in Temperate Ungulate Assemblies, Chapman and Hall, London.

Senft, R. L., Coughenour, M. B., Bailey, D. W., Rittenhouse, L. R., Sala, O. E., and Swift, D. M. (1987). Large herbivore foraging and ecological hierarchies. Bioscience, 37(11), 789-799.

Sinclair, A. R. E. (1985). Does interspecific competition or predation shape the African ungulate community? Journal of Animal Ecology, 54, 899-918.

Sinclair, A. R. E., and Norton-Griffiths, M. (1982). Does competition or facilitation regulate migrant ungulate populations in the Serengeti? A test of hypotheses. Oecologia, 53, 364-369.

Talbot, L. M., and Talbot, M. H. (1963). The wildebeest in western Masailand, East Africa. Wildlife Monographs(12).

Vesey-Fitzgerald, D. F. (1960). Grazing succession among East African game animals. Journal of Mammalogy, 41, 161-172.

Voeten, M. M. and Prins, H.T. (1999). Resource partitioning between sympatric wild and domestic herbivores in East Africa. Oecologia 120: 287-294.

Walker, B. H. (1976). An approach to the monitoring of changes in the composition and utilization of woodland and savanna vegetation. S.Afr.J.Wildl.Res., 1-7.

Table 1: Predicted effects on the overlap of grassland type use, grass height use and grass greenness in relation to resource partitioning, competitive exclusion and grazing successions, as the dry season advances

	1) Resource Partitioning	2) Competitive Exclusion	3) Grazing Succession
Overlap in grazing lawns	- decrease in overlap; non-ruminant and large herbivores have evolved to utilize taller grass	- decrease in overlap; smaller herbivores reduce height; non-ruminant and larger herbivores are unable to subsist	- decrease in overlap as body size increases (similar to resource partitioning)
Overlap in Themeda, woodland and other grasslands or grass species	- decrease in overlap; non-ruminant and larger herbivores have evolved to utilize lower quality patches	- decrease in overlap; narrow mouthed herbivores reduce green leaf in one grassland; non-ruminant and large herbivores must select another	- increase in overlap; smaller herbivores graze in patches previously grazed by larger herbivores
Overlap in grass height	- decrease in overlap; non-ruminant and large herbivores	- decrease in overlap; smaller herbivores reduce height; non-ruminant	- decrease in overlap as smaller herbivores graze

	have evolved to utilize lower quality taller grass; smaller species require higher quality shorter patches	and larger herbivores are unable to subsist	shorter patches previously grazed by larger herbivores
Overlap in grass greenness	- decrease in overlap; non-ruminant and large herbivores have evolved to utilize lower quality grass; smaller species require high quality green patches	- decrease in overlap; smaller and narrow mouthed grazers select and reduce green leaf; non-ruminant and large herbivores graze less green patches	- decrease in overlap; smaller herbivores graze patches with higher leaf:stem ratio due to previous grazing by larger herbivores

Table 2 – Overlap in Foraging Area as assessed by Pianka (1973) index

	Rhino/ Zebra	Rhino/ Wildebeest	Zebra/ Wildebeest	Rhino/ Impala	Zebra/ Impala	Wilde/ Impala
1999						
March-April	0.94	0.9	0.76	0.94	0.83	0.99
May-June	0.62	0.96	0.7	0.9	0.9	0.93
July-August	0.86	0.91	0.9	0.88	0.96	0.81
2000						
May-June	0.99	0.99	0.98			
July-August	0.88	0.99	0.9			

Table 3 – Overlap in Feeding Patch as assessed by Pianka (1973) index

	Rhino/ Zebra	Rhino/ Wildebeest	Zebra/ Wildebeest	Rhino/ Impala	Zebra/ Impala	Wilde/ Impala
1999						
March-April	0.95	0.97	0.88	0.99	0.98	0.93
May-June	0.68	0.83	0.88	0.99	0.73	0.84
July-August	0.87	0.81	0.84	0.97	0.93	0.75
2000						
May-June	0.97	0.97	0.96			
July-August	0.77	0.97	0.84			

Table 4 – Overlap in Grass Height in Feeding Patch as assessed by Pianka (1973) index

Table 4 – Overlap in Grass Height in Feeding Patches

	Rhino/ Zebra	Rhino/ Wildebeest	Zebra/ Wildebeest	Rhino/ Impala	Zebra/ Impala	Wilde/ Impala
1999						
March-April	0.67	0.99	0.73	0.74	0.97	0.76
May-June	0.56	0.81	0.86	0.77	0.8	0.94
July-August	0.53	0.76	0.84	0.75	0.94	0.89
2000						
May-June	0.83	0.88	0.98			
July-August	0.79	0.99	0.86			

Table 5 – Overlap for all resource variables (grassland use in foraging area, feeding patches and grass height use)

Overall Overlap	Rhino/ Zebra	Rhino/ Wildebeest	Zebra/ Wildebeest	Rhino/ Impala	Zebra /Impala	Wilde/ Impala
1999						
March-April	0.60	0.86	0.49	0.69	0.79	0.70
May-June	0.24	0.65	0.53	0.69	0.53	0.73
July-August	0.40	0.55	0.64	0.64	0.84	0.54
2000						
May-June	0.80	0.85	0.92			
July-August	0.54	0.95	0.65			

Table 6 – Proportional Contribution of Grass Species to the Diet of Herbivores

White Rhino		**1999**				**2000**		**Overall**
		March-April	May-June	July-August	**Mean**	May-June	July-August	**Contribution**
Short Spp.:	P.col /U.m	0.36	0.23	0.15	0.25	0.42	0.47	0.33
	D.arg	0.03	0.19	0.09	0.10	0.12	0.11	0.11
	Sp.n	0.03	0.07	0.00	0.03	0.11	0.07	0.06
	Total	0.41	0.51	0.32	0.38	0.66	0.66	0.50
Woodland:	P.max	0.26	0.14	0.30	0.23	0.15	0.14	0.20
Tall Spp.	Th.tr	0.18	0.14	0.19	0.17	0.02	0.01	0.11
Wildebeest		**1999**				**2000**		**Overall**
		March-April	May-June	July-August	**Mean**	May-June	July-August	**Contribution**
Short Spp.:	P.col/U.m	0.28	0.20	0.07	0.18	0.44	0.37	0.27
	D.arg	0.07	0.11	0.00	0.06	0.10	0.10	0.08
	Sp.n	0.16	0.07	0.02	0.08	0.07	0.08	0.08
	Total	0.51	0.37	0.09	0.32	0.62	0.55	0.43
Woodland:	P.max	0.19	0.13	0.26	0.19	0.14	0.08	0.16
Tall Spp.	Th.tr	0.16	0.15	0.26	0.19	0.07	0.12	0.15
Other Spp.	Setaria/Cenchrus	0.00	0.17	0.00	0.06	0.02	0.07	0.05
	E.sup	0.00	0.07	0.13	0.06	0.03	0.03	0.05
Zebra		**1999**				**2000**		**Overall**
		March-April	May-June	July-August	**Mean**	May-June	July-August	**Contribution**
Short Spp.:	P.col/U.m	0.26	0.09	0.08	0.14	0.40	0.31	0.23
	D.arg	0.02	0.00	0.02	0.01	0.06	0.00	0.02
	Sp.n	0.02	0.00	0.00	0.01	0.06	0.02	0.02
	Total	0.29	0.09	0.10	0.16	0.52	0.33	0.27
Woodland:	P.max	0.24	0.27	0.54	0.35	0.22	0.41	0.34
Tall Spp.	Th.tr	0.21	0.20	0.14	0.18	0.06	0.06	0.13
Other Spp	Setaria	0.00	0.09	0.02	0.04	0.03	0.04	0.04
	E.sup	0.02	0.11	0.04	0.06	0.02	0.00	0.04
Impala		**1999**				**2000**		**Overall**
		March-April	May-June	July-August	**Mean**	May-June	July-August	**Contribution**
Short Spp.	P.col/U.m	0.29	0.34	0.23	0.29			
	D.arg	0.03	0.10	0.02	0.05			
	Sp.n	0.00	0.02	0.04	0.02			
	Total	0.32	0.46	0.30	0.36			
Woodland:	P.max	0.26	0.22	0.47	0.32			
Tall Spp.	Th.tr	0.32	0.12	0.09	0.17			
Other Spp.	Both	0.03	0.10	0.09	0.07			

Table 7 – Acceptability of Grass Species by Herbivores

(Acceptability is the proportion of the number of times the grass species was eaten, divided by the number of times the grass species was found in the feeding station quadrat (number in brackets))

White Rhino	**1999**				**2000**		**Overall**
	March-April	May-June	July-August	**Mean**	May-June	July-August	**Acceptability**
Short species	0.44 (36)	0.49 (43)	0.46 (28)	0.46 (107)	0.90 (78)	0.96 (48)	0.71 (233)
P. max	0.83 (12)	0.50 (12)	0.89 (18)	0.74 (42)	0.89 (18)	1.00 (10)	0.83 (70)
Themeda	0.78 (9)	0.35 (17)	0.67 (15)	0.60 (42)	0.67 (3)	1.00 (1)	0.58 (45)
Other	0.00 (4)	0.57 (7)	0.36 (11)	0.31 (22)	1.00 (3)	1.00 (7)	0.56 (32)

Wildebeest	**1999**				**2000**		**Overall**
	March-April	May-June	July-August	**Mean**	May-June	July-August	**Acceptability**
Short species	0.47 (59)	0.45 (38)	0.17 (30)	0.36 (127)	0.85 (71)	0.69 (58)	0.59 (256)
P. max	0.85 (13)	0.67 (9)	0.78 (18)	0.77 (40)	0.88 (16)	0.67 (9)	0.78 (65)
Themeda	0.56 (16)	0.58 (12)	0.78 (18)	0.64 (46)	0.78 (9)	0.90 (10)	0.71 (65)
Other	0.13 (8)	0.88 (16)	0.77 (13)	0.59 (37)	0.37 (19)	0.56 (16)	0.57 (72)

Zebra	**1999**				**2000**		**Overall**
	March-April	May-June	July-August	**Mean**	May-June	July-August	**Acceptability**
Short species	0.35 (52)	0.16 (25)	0.25 (20)	0.25 (97)	0.80 (56)	0.59 (29)	0.49 (182)
P. max	0.71 (21)	0.75 (16)	0.87 (31)	0.78 (68)	0.86 (22)	0.88 (24)	0.82 (114)
Themeda	0.59 (22)	0.64 (14)	0.70 (10)	0.64 (46)	0.71 (7)	0.75 (4)	0.65 (57)
Other	0.36 (11)	0.80 (15)	0.46 (13)	0.54 (39)	0.56 (9)	0.23 (13)	0.49 (61)

Impala	**1999**				**2000**		**Overall**
	March-April	May-June	July-August	**Mean**	May-June	July-August	**Acceptability**
Short species	0.26 (47)	0.53 (36)	0.52 (27)	0.41 (45)	-	-	-
P. max	0.50 (20)	0.53 (17)	0.85 (26)	0.65 (41)	-	-	-
Themeda	0.67 (18)	0.84 (6)	0.44 (9)	0.64 (21)	-	-	-
Other	0.18 (11)	0.45 (11)	0.63 (8)	0.40 (12)	-	-	-

Figure 1a – Rainfall in western Imfolozi Nature Reserve from 1998 to 2000

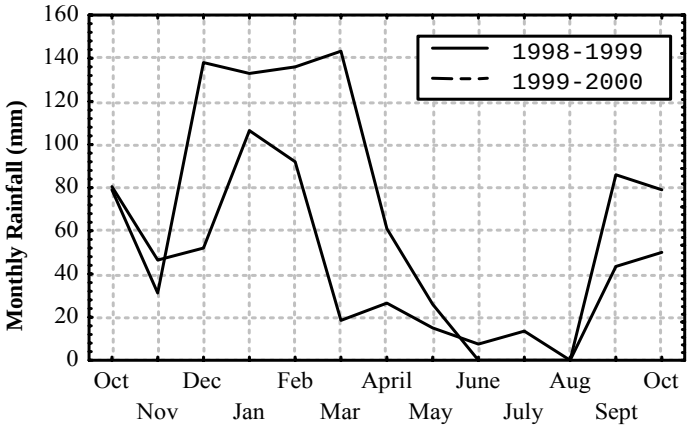


Figure 1b – The proportion of grass that was green, mainly green, mainly brown and brown in the dry season of 1999 and 2000

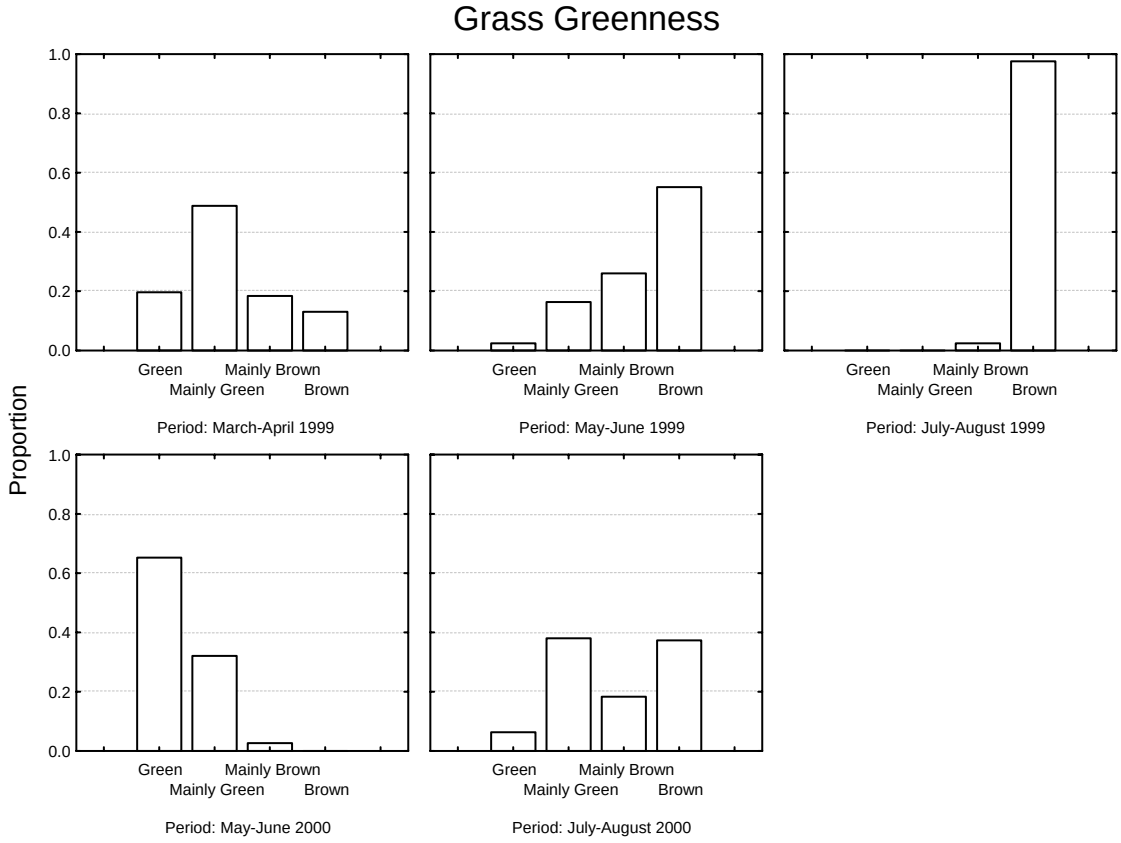


Figure 2a – Average grass height of <u>foraging areas</u> utilized by the herbivores (categories: grazing lawns, *Themeda* grassland, woodland grassland)

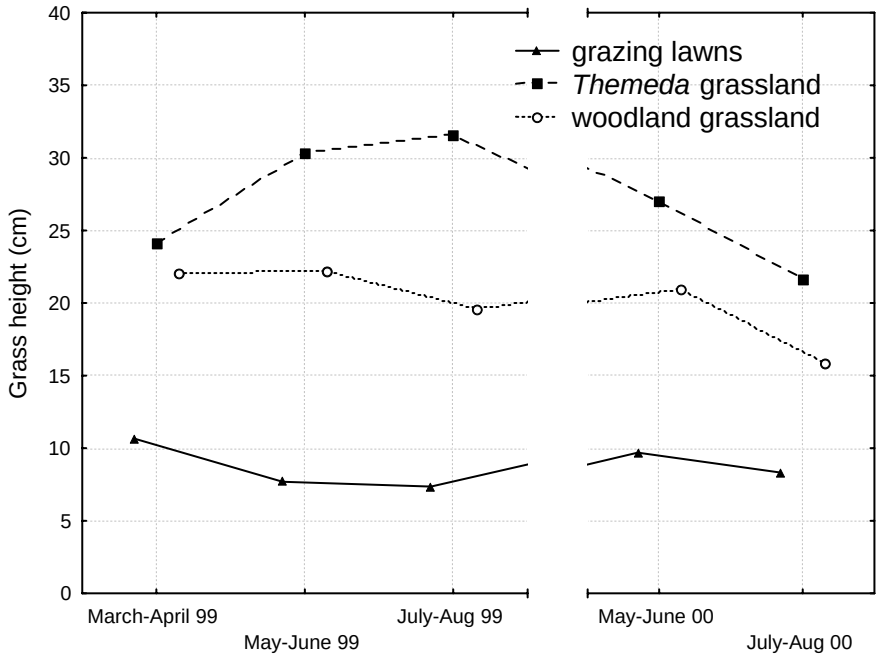


Figure 2b - Average grass height of <u>feeding patches</u> utilized by the herbivores (categories: grazing lawns, *Themeda* grassland, woodland grassland)

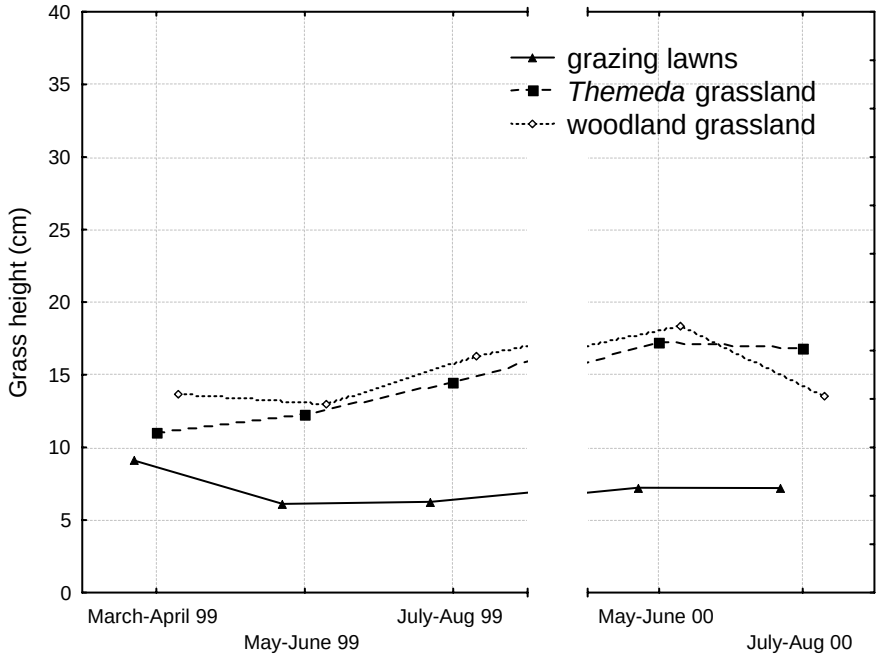


Figure 3 – Use of Grassland Types in Foraging Areas (similar distributions have the same letter)

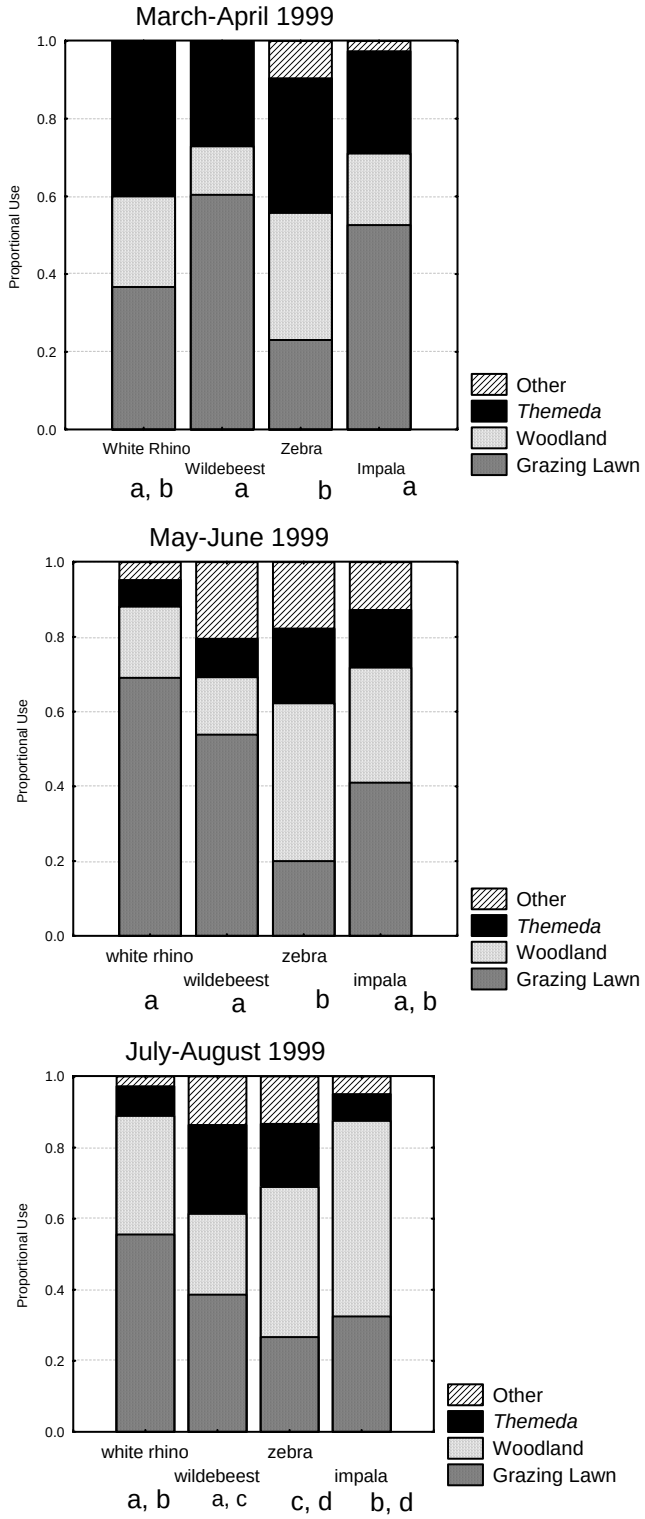


Figure 3 (cont'd)

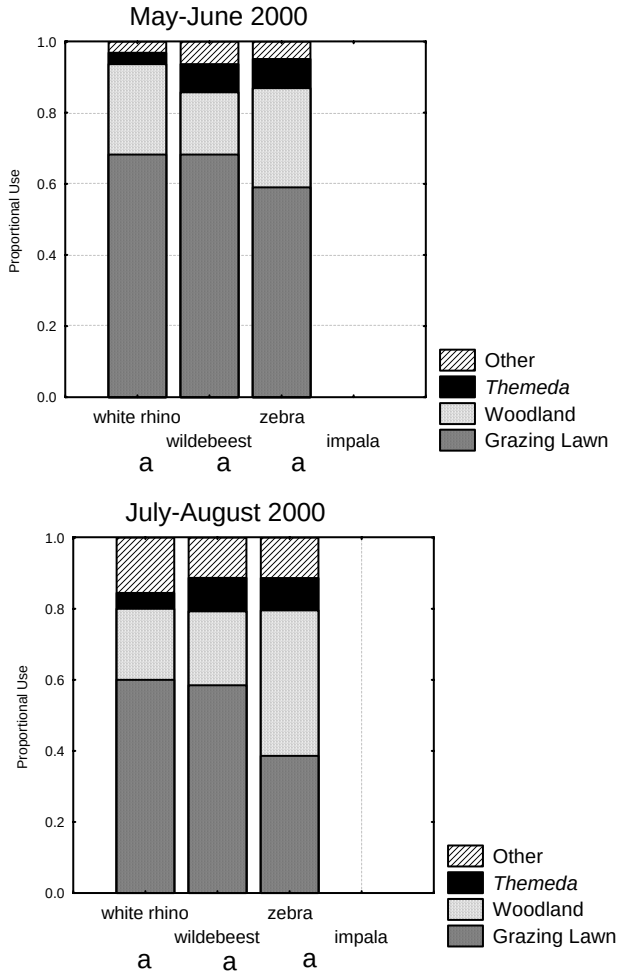


Figure 4 – Use of Grassland Types in Feeding Patches (similar distributions have the same letter)

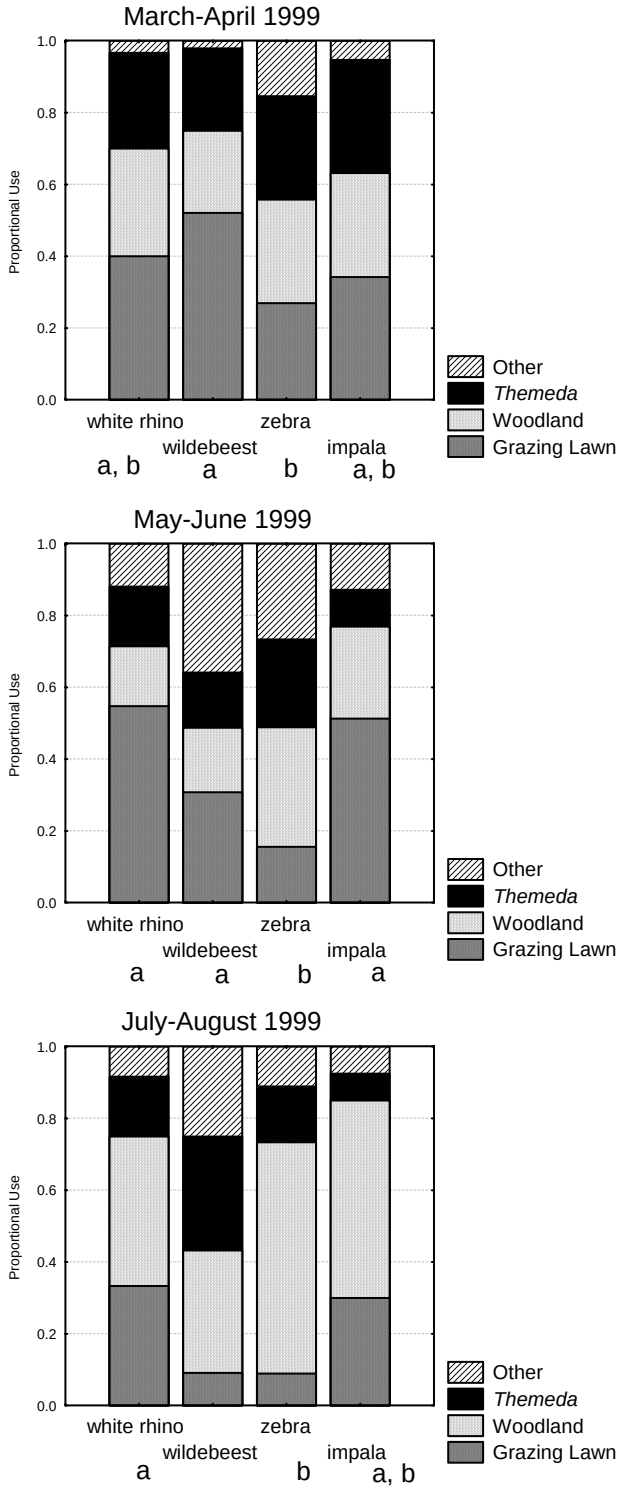


Figure 4 (cont'd)

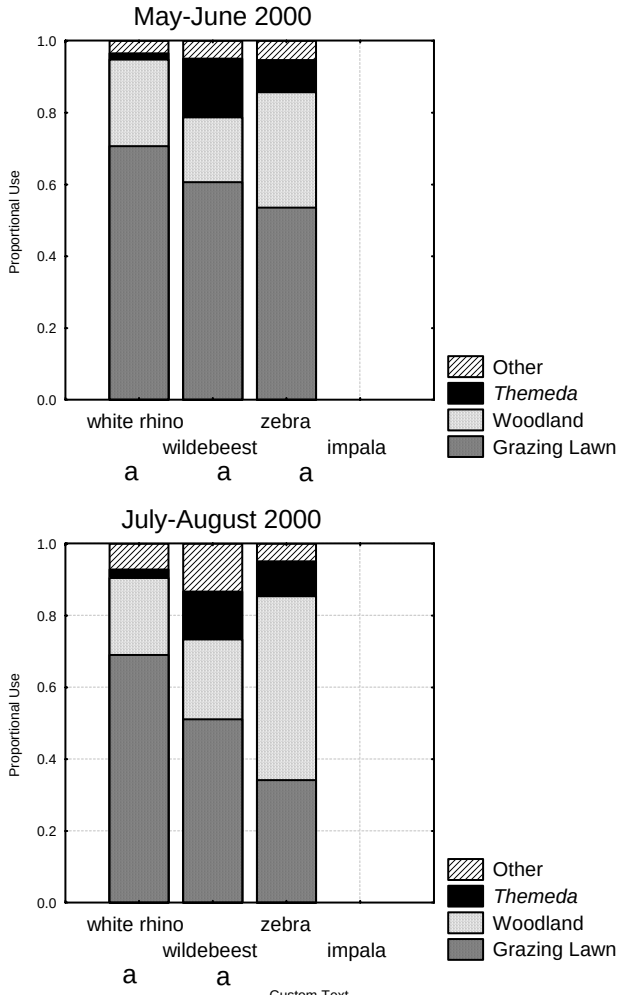


Figure 5 – Proportion of grazing lawn species chosen in <u>feeding patches</u>, when herbivores were found using grazing lawns in <u>foraging areas</u>

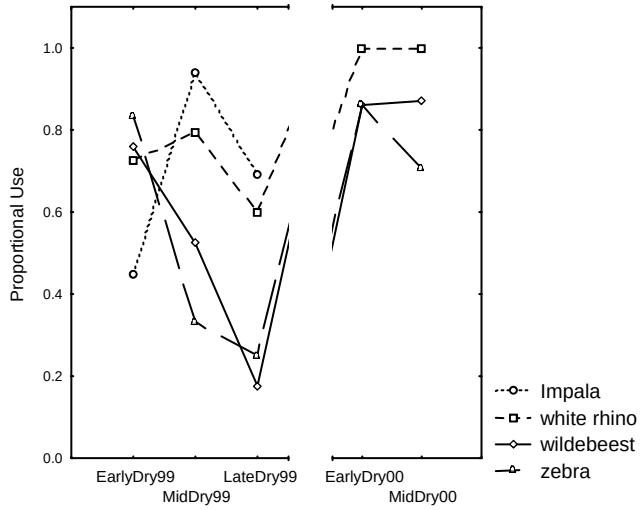


Figure 6 – The proportion of grass height categories utilized by herbivores (categories: 21+, 11-20 cm, 6-10 cm, < 6 cm) (similar distributions have the same letter)

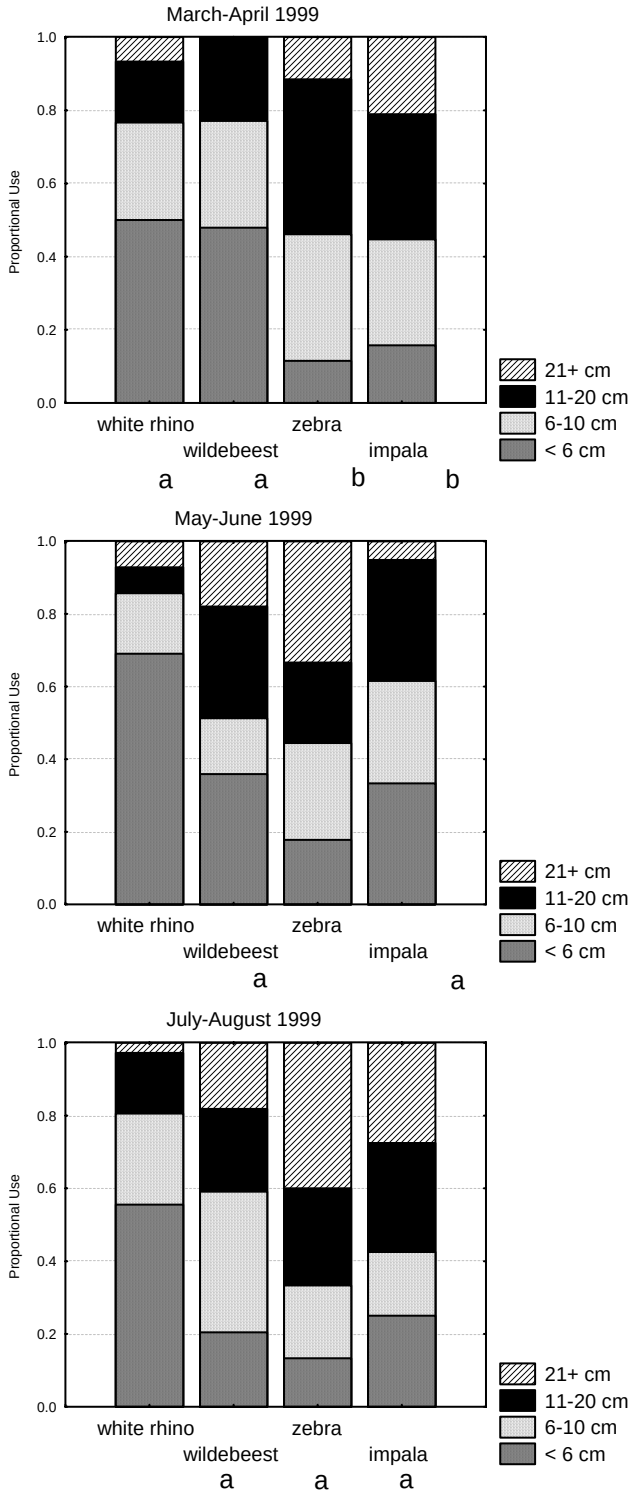


Figure 6 (cont'd)

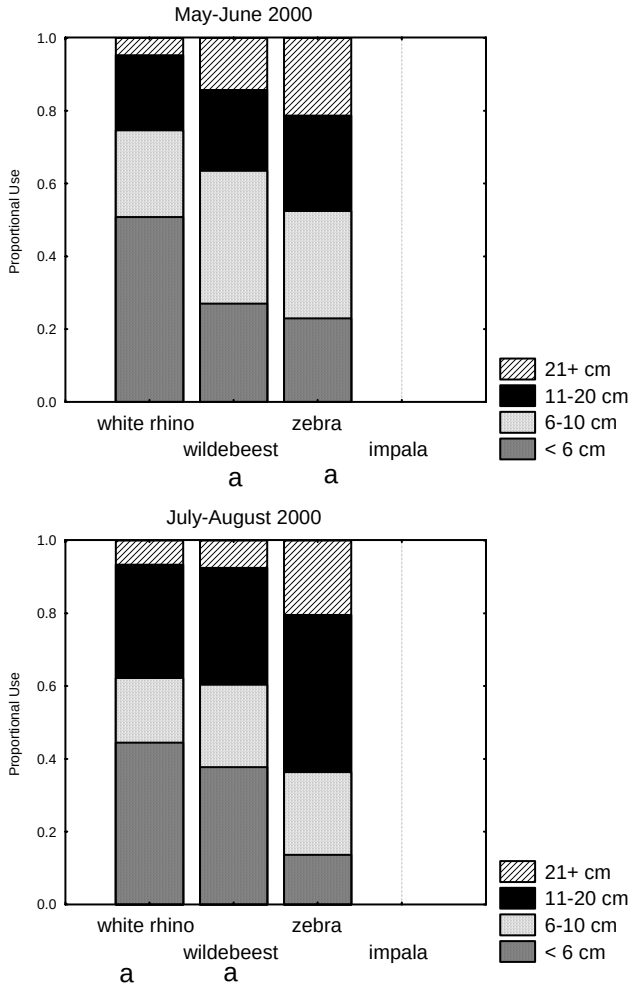


Figure 7 – Correspondence Analysis including grass height (<6cm: 6-10cm: 11-20cm: >21cm), herbivore (white rhino: WR, wildebeest: WD, zebra: Z, impala: IMP), grassland use in foraging "area" (grazing lawns: L-a, woodland: W-a, *Themeda*: T-a, other: O-a), and grassland use in feeding "patch" (grazing lawns: L-p, woodland: W-p, *Themeda*: T-p, other: O-p)

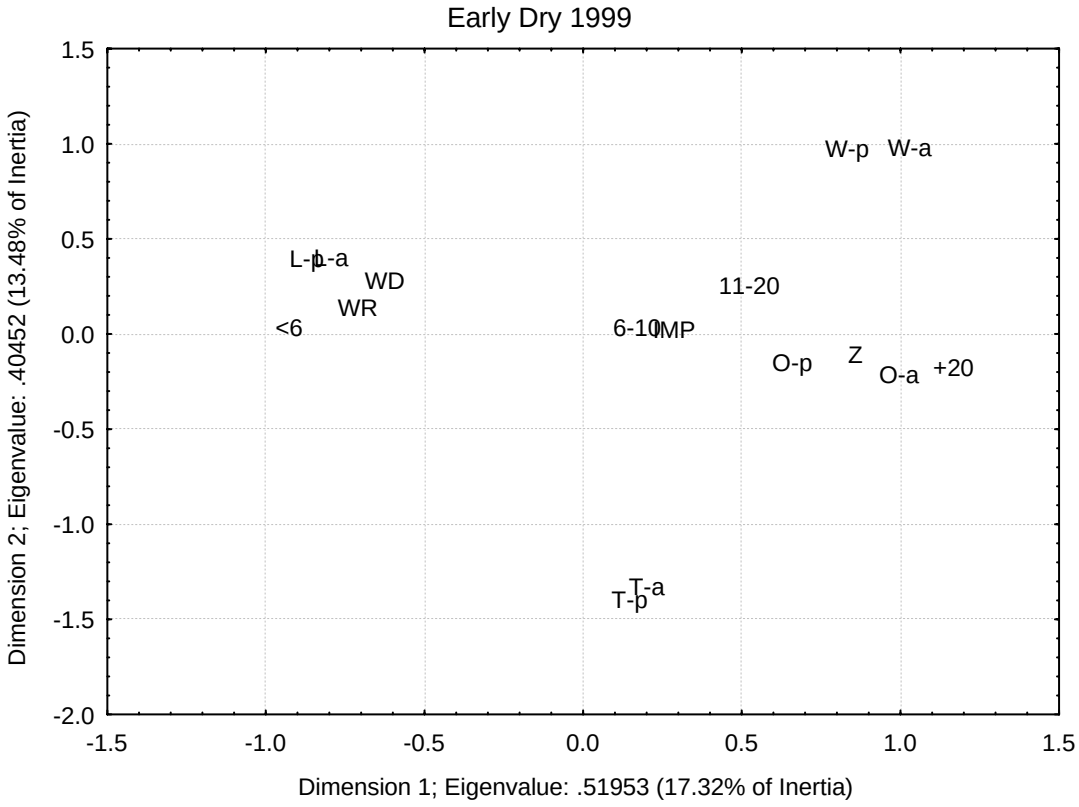
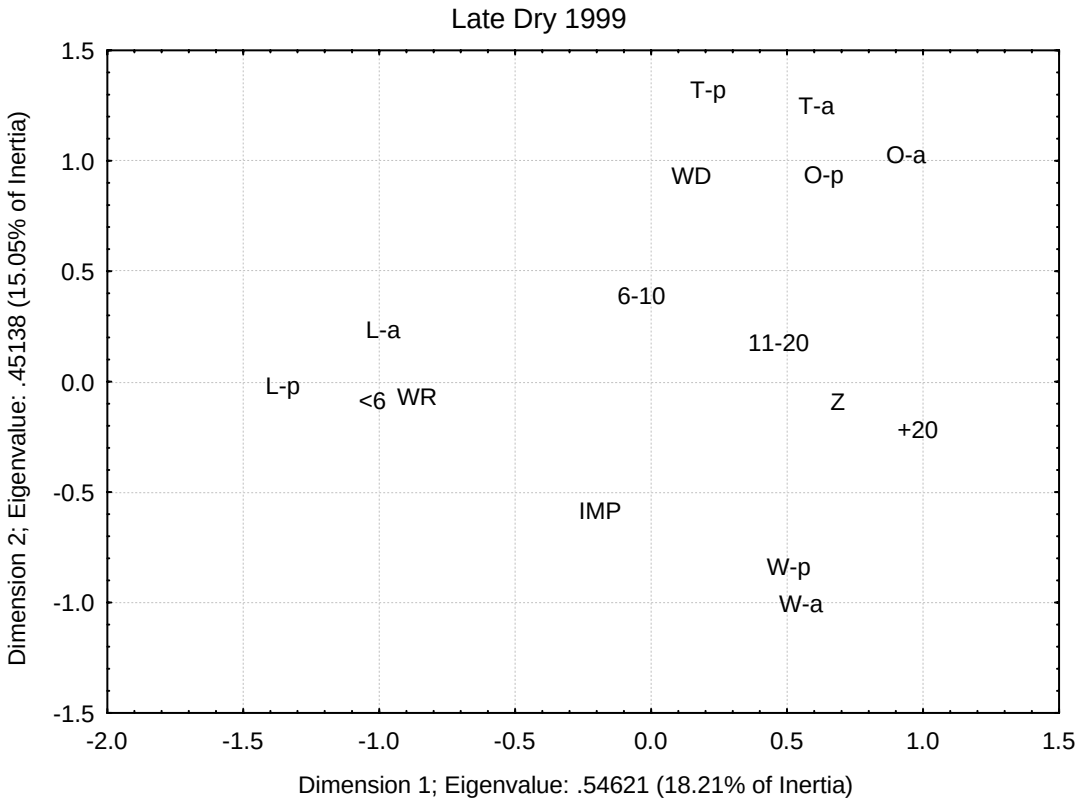
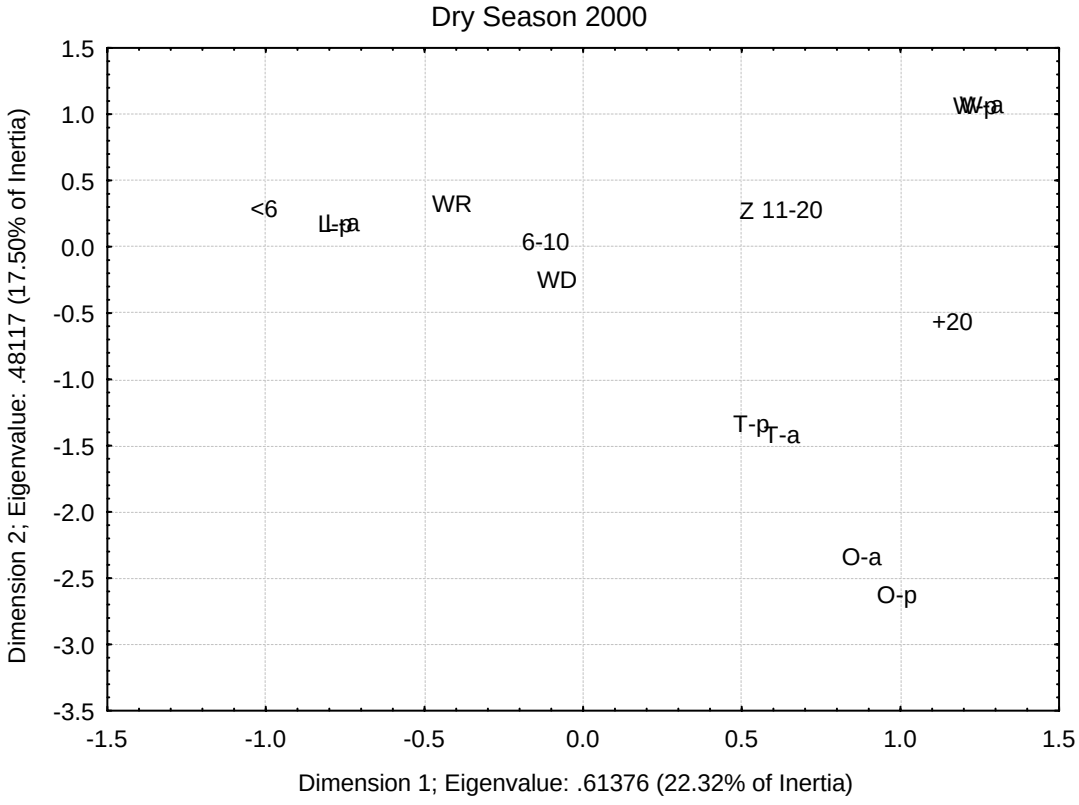


Figure 7
– Correspondence Analysis (cont'd)





CHAPTER FIVE

The effect of white rhino grazing on grazing lawns in Hluhluwe-iMfolozi Park, South Africa

By Randal Arsenault

INTRODUCTION

Murray and Illius (1996) suggest that grazing lawns may be important in terms of interspecific resource competition between species, where the grazing by some species may negatively affect others through a reduction in grass height or grass quality. Alternatively, by reducing grass biomass one species may benefit another by facilitating access to forage of a suitable height or quality (Vesey-Fitzgerald 1960; Bell 1970; Bell 1971; McNaughton 1976). The relative importance of these two processes in structuring species assemblages remains unclear.

The highest density of white rhino in Africa are found in Hluhluwe-iMfolozi Park, South Africa (32.7 kg/ha). White rhino have the ability to transform tall grass areas to short grass areas (grazing lawns) (Owen-Smith 1988). In the previous chapters I showed that white rhino also heavily utilize grazing lawns, which may be detrimental or beneficial to other grazers in HiP, such as wildebeest, zebra, and impala. White rhino grazing may competitively exclude other herbivores from grazing lawns in the dry season, or facilitate other herbivores by increasing the quality of grazing lawns in the wet season. In addition, the smallest species, impala (and nyala) may have the ability to reduce the quality of grazing lawns, through increased grazing selectivity for green grass in the dry season.

The following paper documents an experiment to determine the effect of white rhino grazing on the height, greenness and percentage of nitrogen of grazing lawns in iMfolozi Park, South Africa. Exclosure plots were designed and erected on grazing lawns in order to exclude white rhino, without excluding other grazing herbivores. The use of exclosures were compared with the use of open control areas in which white rhino can

graze. I predict that in the wet season, white rhino grazing facilitates other herbivore species by increasing grass re-growth and sward quality of grazing lawns. Therefore, all herbivores are expected to graze open control areas more than areas where white rhino are excluded. However, in the dry season white rhino are expected to out compete other herbivores as grass height is reduced. Therefore, I predict that other herbivores will graze in areas where white rhino are excluded, compared to open control areas.

METHODS

The design of the experiment included three site (plot) replicates with similar soil and grazing lawn species composition, and two treatments within each site: i.e. open control areas and white rhino exclosure areas. The three exclosure plots were erected in August and September 1999, in the western section of Hluhluwe-iMfolozi Park, Kwa-Zulu Natal, South Africa (28° 20' S, 31° 51' E). Each plot consisted of a 40 x 40 m white rhino exclosure and a marked 40 x 40 m open area for the control, immediately adjacent.

To exclude white rhino, a thick steel cable was placed around the 40 x 40 m exclosure area, 60 cm from the ground. White rhino are unable to lift their feet far off the ground, and therefore are inhibited to walk over the cable into the exclosure. Herbivores such as zebra, wildebeest and buffalo should not be deterred from walking over the cable, and smaller species, such as impala, nyala and warthog can walk or crawl under the cable or jump over it.

The sites for the plots were chosen based on their similarity in predominant tree species (*Acacia nigrescens*), short grass species composition, and soil type. The sites were at least 1 km apart but no more than 3 km away from each other. The sites were named Upper Thobothi, Lower Thobothi and Mbuzane. The most common short grass species in iMfolozi are *Panicum coloratum, Urochloa mosambicensis, Sporobolus nitens,* and *Digitaria argyograpta.*

Data collection on grass height and greenness was collected for February, March, June, July, August, October, November and December in 2000. . In 2001 data was collected on January 3rd and January 18th, and in February, March, April, May, and

August. Data was mainly collected by two field assistants, as I was unable to be in the field the entire year.

Data collection consisted of 20 samples per treatment. The 20 samples, per treatment, were taken randomly by dividing each treatment into 1 m grids and labelling the grids. Then 20 grids per treatment were picked randomly by computer. At each treatment, I would start at one corner, designated grid A1, and pace one meter at a time (one long stride at a time), until I reached designated randomly picked grid. This was repeated for all 20 samples per treatment each month.

Grass height for each 1 m grid was measured using a disc pasture meter (Bransby and Tainton 1977). I then placed a 25 cm x 25 cm quadrat in front of my two feet. A small quadrat was used (instead of a 1 m^2 quadrat), to reduce the effect of clipping grass samples on grass height within the treatments. Species composition was determined by estimating the percentage of aerial cover for each grass species within the quadrat. Species composition was only determined in February 2000 and January 2001, i.e. during the wet season at the start of the sampling year. The species composition for each of the three sites was determined by averaging the percentages of species for the 20 samples in the control areas and the 20 samples in the exclosure treatments.

Five of the twenty grids per treatment were also picked at random to collect grass clip samples. Within the quadrat of the five grids, grass was clipped close to ground level, approximately 2 cm in height. The grass was placed in a paper bag and labelled and brought back to the lab. For each grass clipped sample, green and brown grass were separated by hand, and put into separate paper bags and labelled. The green and brown grass was then dried in an oven and weighed. The percentage of green versus brown grass was averaged for each treatment, and used in the analysis. Each sample of green and brown grass per grid was then milled to send away to a lab for nitrogen analysis. Due to the cost of analysis, only three samples (out of five) per treatment were analysed for nitrogen for the wet season of 2000/2001, and the months October 2000, January 2001 and March 2001. The wet season is when grazing facilitation by increased sward quality would occur.

The presence and number of grazing herbivore dung piles were recorded to determine whether herbivores were found within each treatment or not. Within all

treatments, each 1 m^2 grid line was walked and each dung pile was recorded as fresh, partly dry or dry. The grid number and the dung of each herbivore species were also recorded. Only fresh and partly dry dung samples were recorded, to prevent recounting of dung piles from previous months. Dung dries very quickly such that each dung sample per month is independent of other months. Due to the difficulty of determining impala versus nyala dung, these herbivores were combined into one category.

Grass Species composition

The major grass species present in Upper Thobothi was *Panicum coloratum* (38%), *Urochloa mosambicensis* (28%) and *Digitaria argyograpta* (14%), in Lower Thobothi was *Urochloa mosambicensis* (53%) and *Panicum coloratum* (32%), and in Mbuzane was *Panicum coloratum* (42%) and *Urochloa mocambiscensis* (39%).

DATA ANALYSIS

The design of this experiment involves repeated measures over time of grass height and grass greenness (i.e. the many data points in each treatment are not independent of each other due to spatial auto-correlation). A two way ANOVA with a repeated measures design (Quinn and Keough 2002) was used to test the statistical differences between grass height and grass greenness in Statistica (2000). Tukey HSD was used for all post hoc analyses. Data on grass height was log transformed, and data on grass greenness was arcsine transformed. A one way ANOVA was used to analyse the nitrogen content on green leaves between the exclosure areas and control areas in the wet season of 2001. A generalized linear model, with a Poisson log link, was used to analyze the difference in dung counts of species between the exclosure and control areas. Seasons were determined by rainfall, as Wet 2000 (February-June 2000), Dry 2000 (April-August 2000), Wet season 2000/2001 (October 2000-February 2001), and Dry 2001 (March-August 2001). The mean and 95% confidence limits are reported.

.

RESULTS

Grass height of plots

There was a significant difference in the grass heights between the treatments and between the plots ($F_{6, 690} = 3.66$, $p < 0.001$). Grass height was lower in open control plots compared to exclosures where white rhino were excluded in all seasons ($F_{3, 690} = 3.90$, $p < 0.009$) (Figure 1). Grass height changed seasonally over the course of the experiment in relation to rainfall, where height was greatest in the wet periods compared to the dry periods (Figure 1). Grass height was greatest in the high rainfall year and wet season of 2000 (February-March 2000) (mean = 9.6 cm, CL 9.0-10.1 cm), and declined in dry season 2000 (June – August 2000) (mean = 6.4 cm, CL = 6.1-6.8 cm), wet season 2001 (October 2000 – February 2001) (mean = 6.1cm, CL = 5.8, 6.3cm) and dry season of 2001 (March-August 2001) (mean = 4.3 +- 0.2 cm).

Grass greenness

There was no significant difference or interaction in grass greenness between the plots and between control and exclosure areas ($F_{6,126} = 0.188$, $p = .980$). Grass greenness did change seasonally over the course of the experiment ($F_{3,126} = 56.26$, $p < 0.001$), where greenness was greatest in the wet seasons.

Nitrogen content

In the Wet 2001, there was no difference detected in the nitrogen content of green leaves, between open areas (mean = 1.45, CL=1.28–1.62) and where white rhino were excluded (mean=1.36, CL=1.2–1.52) ($F_{4,28}=.676$; $p=.6142$). This difference may have been smaller than we were able to detect, due to the low number of samples used for analysis, as well as the increase in variance due to the number of grass species used in each sample.

Dung counts

There were significantly more dung piles of zebra ($X^2 = 11.97$, df = 1, $p < 0.001$) and wildebeest ($X^2 = 25.166$, df =1, $p < 0.001$) found in the open control areas compared to exclosure areas (Figure 2). There was no significant difference in the number of dung piles within control areas and exclosure areas impala/nyala ($X^2 = 0.953$, df =1, $p = 0.329$), however more dung piles of impala/nyala were found in the control areas during wet 2001 (Figure 2). More wildebeest and zebra dung piles were found in comparison to impala/nyala, and fewer zebra dung piles were found compared to wildebeest. More dung piles of wildebeest, zebra and impala/nyala were found in dry period of 2001, compared to other periods (Figure 2).

DISCUSSION

Grass height was significantly shorter in areas open to all species grazing than in the white rhino exclosures. Whether this effect was due primarily to white rhino grazing is unclear. More wildebeest and zebra dung piles were found in open grazing areas compared to exclosure areas. This suggests that wildebeest and zebra may have been inhibited from in grazing exclosure areas due to the cable around these plots. Therefore, the difference in grass height between open areas and exclosures can not be attributed to white rhino alone. Impala and nyala did not appear to be inhibited by the cable, as there was no difference in their dung piles between the treatments. If wildebeest, zebra and other larger grazers were inhibited by the cable, then the changes in grass height within the exclosures may primarily be due to the grazing of impala and nyala.

The main limitation of this study is relating dung counts to actual grazing of grass. Direct observations of grazing would have been ideal, however, it was decided that physically monitoring the sites for two years was too time consuming and that purchasing cameras was not financially possible. The presence of dung indicates the presence of the species, but does not indicate whether the animal grazed grass. Herbivores may be moving through and area, or resting. Grazing lawns are open areas with few trees, and ideal for the

detection and avoidance of predators. Wildebeest, zebra and impala may be using these areas to rest between feeding.

1) Competition through the reduction of grass quantity

In both dry seasons, grass height was reduced in open control areas compared to exclosure areas. In the driest year, grass height in the open areas was grazed below 5 cm in all plots. In Chapter 2 and 3, I showed that white rhino grazed heights below 6 cm more than zebra, wildebeest and impala, and that evidence suggests zebra and wildebeest were excluded from grazing lawns through a reduction in grass height. Therefore I would expect that wildebeest and zebra would use exclosure areas more than control areas, due to the greater height and availability of grass. However, observations of dung piles found that wildebeest and zebra utilized control areas more than exclosure areas. This was shown most convincingly in dry 2001, which is also when grass height was the shortest. There was no difference detected in grass greenness and nitrogen between the treatments. Therefore wildebeest and zebra were most likely inhibited from grazing the exclosure areas due to the cable.

Impala and nyala utilized control areas and exclosure areas comparably and did not appear to be affected by the presence of the cable. This also means that impala and nyala did not show a preference for grazing the taller grass in the exclosures. As discussed in Chapter 3, impala utilized grazing lawns longer into the dry season, similar to white rhino. Impala did not appear to be excluded by the reduction in grass height in grazing lawns, compared to zebra and wildebeest (Chapter 3). However, impala and nyala have been shown in other studies to mainly eat browse during the dry seasons (Jarman and Sinclair 1979; Estes 1991). The reduction in grass height in the exclosure plots, of this experiment, suggest impala/nyala are heavily grazing as well.

2) Competition through the reduction of grass quality

Another potential mechanism of competition is where small and/or selective grazers reduce the green leaf in a sward to the detriment other species (Murray and Illius

1996; 2000). Less wildebeest and zebra dung piles were found in exclosure areas compared to open control areas, whereas there was no difference for impala/nyala. This suggests the predominant grazers within the exclosures was impala/nyala. Impala are selective grazers for green leaf (Jarman and Sinclair 1979). It is therefore a possibility that fewer wildebeest and zebra utilize exclosures be due to the reduction of green leaf by impala and nyala. This effect would be most pronounced in the dry season when greenness is declining. However, no difference was found in grass greenness between the exclosures and open areas during the dry and wet seasons. Therefore there is little evidence that impala and nyala reduced the green leaf of a sward to the detriment of others.

3) Facilitation through increasing grass quality

It has been shown that grazing in the wet season can stimulate grass re-growth leading to an increase in grass nutrients (McNaughton 1976; Gordon 1988; Arsenault and Owen-Smith 2002), and that the quality of green leaf can depend on grazing pressure in the dry season (Murray and Illius 1996). As white rhino is the predominant grazer of short grasslands in iMfolozi, we would expect that areas grazed by all species and white rhino, would be more nutritious that areas excluding white rhino over the dry and wet seasons.

The nitrogen content of green leaves in the wet season of 2001 did not differ between exclosures and open areas. Therefore there is little evidence from my experiment to suggest that grazing by all species is increasing the quality of grass compared to exclosure areas. This may mean that facilitation in grazing lawns is not occurring in open areas, or that the grazing pressure in the exclosure areas is high enough where facilitation is occurring in both treatments. Unfortunately, without further information we cannot know the answer. One limitation is that only three samples of green leaf per treatment were analysed for nitrogen, and the green leaves were not separated for each grass species. Such that the variance in the data may have been due to the different percentage of grass species in the samples, or the sample size was too small to detect differences.

CONCLUSION

This experiment was undertaken to study the affect of white rhino grazing on grazing lawns and the potential for competition and facilitation of other grazers. Unfortunately the cable exclosure areas appear to have excluded zebra and wildebeest, as well as white rhino. Grass height was found to be lower in open control areas where all species grazed, compared to exclosures. However, there was no difference found between the treatments in grass greenness in all periods, or nitrogen content of leaves during the wet season. I did not find evidence for either competition through reduction in grass height, or the reduction in green leaf and quality, in the dry season. I also did not find evidence that white rhino grazing increased the quality of grazing lawns in the wet season. The results of this experiment was likely influenced by the failure of the design to exclude only white rhino from grazing lawns.

REFERENCES

Anderson, G. D., and Walker, B. H. (1974). Vegetation composition and elephant damage at Sengwa Wildlife Research Area, Rhodesia. J.sthn.Afr.Wildl.Mgmt.Ass., 4, 1-14.

Arsenault, R. and Owen-Smith, N. (2002). Facilitation vs. competition in grazing herbivore assemblages. Oikos 97:313-318.

Bell, R. H. V. (1970). The use of the herb layer by grazing ungulates in the Serengeti. Animal Populations in Relation to their Food Resources, A. Watson, ed., Blackwell Scientific Publications, Oxford, 111-124.

Bell, R. H. V. (1971). A grazing ecosystem in the Serengeti. Scientific American, 224, 86-93.

Bransby, D. I., and N.M. Tainton (1977). The Disc Pasture meter: possible applications in grazing management. Proceeding of the Grassland Society of Southern Africa. 12: 115-118.

Illius, A. W., and Gordon, I. J. (1987). The allometry of food intake in grazing ruminants. Journal of Animal Ecology, 56, 989-999.

Jarman, P. J., and Sinclair, A. R. E. (1979). Feeding strategy and the pattern of resource partitioning in ungulates. Serengeti: Dynamics of an Ecosystem, A. R. E. Sinclair and M. Norton-Griffiths, eds., University of Chicago Press, Chicago.

McNaughton, S. J. (1976). Serengeti migratory wildebeest: facilitation of energy flow by grazing. Science, 191, 92-94.

McNaughton, S. J. (1985). Ecology of a grazing ecosystem: the Serengeti. Ecological Monographs, 55(3), 258-294.

Murray, M. G., and Illius, A. W. (1996). Multi-species grazing in the Serengeti. The Ecology and Management of Grazing Systems, J. Hodgson and A. W. Illius, eds., CAB International, 247-272.

Owen-Smith, N. (1988). Megaherbivores: The influence of very large body size on ecology, Cambridge University Press, Cambridge.

Quinn G.P. and J. Keough (2002). Experimental design and data analysis for biologists. Cambridge University Press.

Vesey-Fitzgerald, D. F. (1960). Grazing succession among East African game animals. Journal of Mammalogy, 41, 161-172.

Figure 1 - Seasonal grass height changes between white rhino exclosures and open control areas in Lower Thobothi, Mbuzane, and Upper Thobothi. Means and 95% CL's reported.

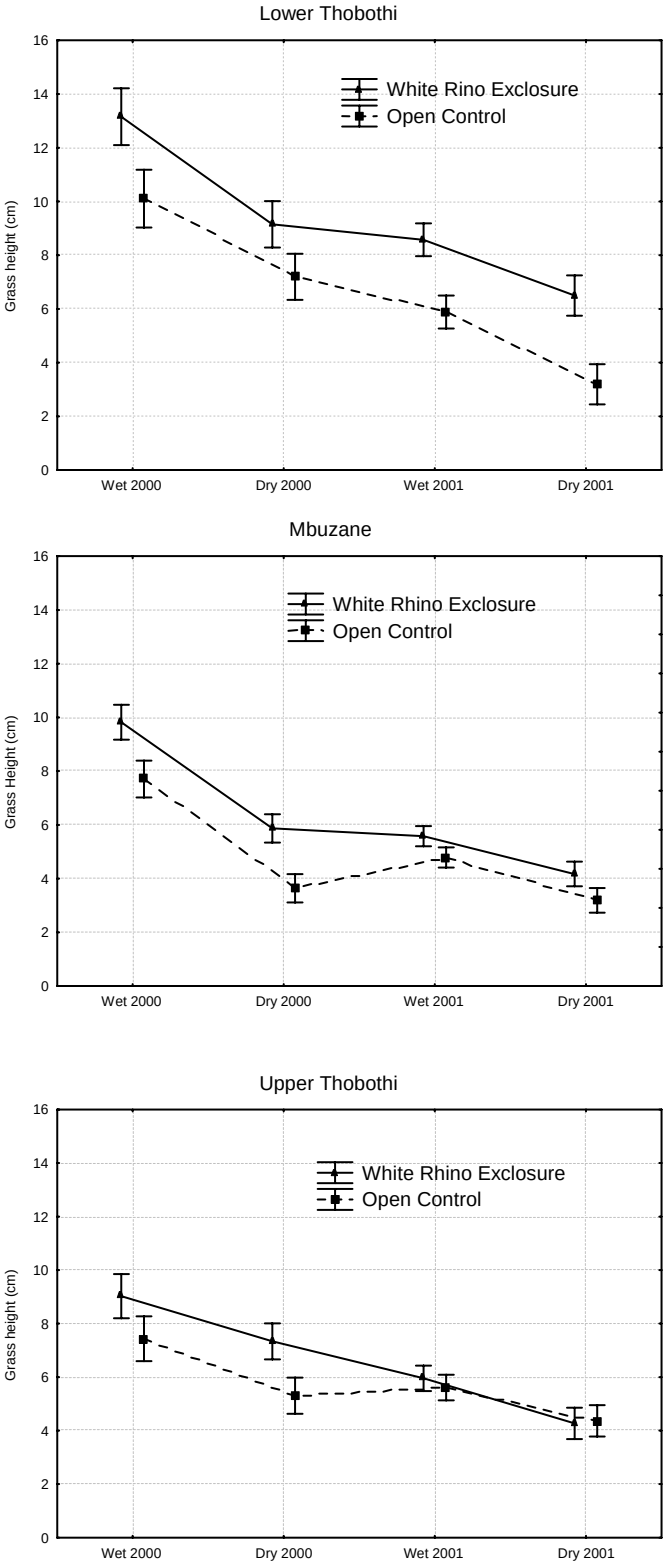
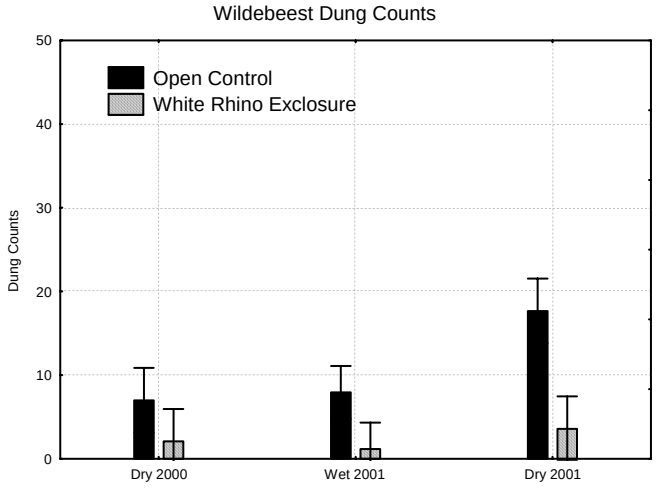
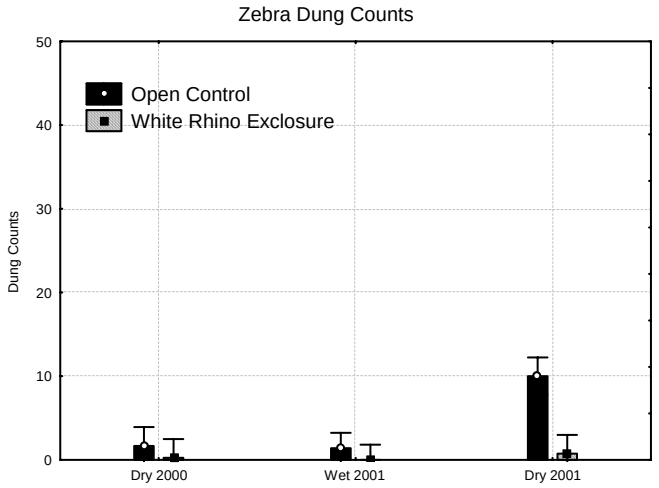
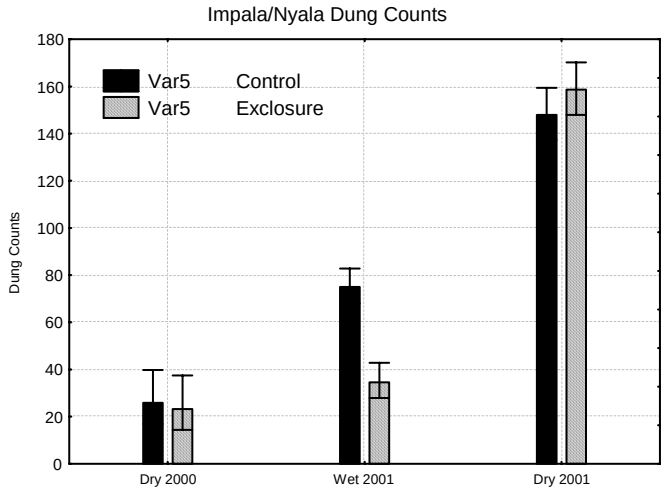


Figure 3- Seasonal dung counts in white rhino exclosures and open control areas for wildebeest, zebra and impala/nyala. Means and 95% CL's reported.







Chapter Six

CONCLUSIONS

At the beginning of this thesis, I outlined the major questions addressed in my study: 1) What are the mechanisms of facilitation and competition for grass resources, and where and when do they occur (Chapter Two, Chapter Four)?; 2) What evidence is there that facilitation or competition affect the nutrition and populations of herbivores (Chapter Two, Chapter Four)?; 3) Do species partition resources in relation to body size (Chapter Three)?; 4) Do white rhino and impala competitively excluded zebra and wildebeest from grazing lawns in the dry season, through a reduction in grass height (Chapter Four, Chapter Five)?; 5) Do impala competitively excluded white rhino, zebra and wildebeest from grazing lawns and medium-tall swards through a reduction in green leaf (Chapter Four, Chapter Five)? 6) Do zebra and white rhino facilitate wildebeest and impala in the dry season, by reducing height in tall swards and increasing access to green leaf (Chapter Four)?; and 7) Do white rhino facilitate other herbivores by increasing the quality of grazing lawns in the wet season? (Chapter Five).

I feel this research has successfully answered the majority of these questions or has clarified the main issues which need to be addressed in the future. The following are the original contributions this thesis makes to science. Please note that Chapter 2 and Chapter 3 were co-authored by Norman Owen-Smith with the aim of publication. The vast majority of these chapters are my work, writing and ideas, and the culmination of numerous drafts. Dr. Owen-Smith contributed in the final drafts helping to edit and tighten the overall story. For example, in Chapter Two, I reviewed the literature and clarified our understanding of the mechanisms of facilitation. I concluded that evidence for facilitation through stimulation of grass re-growth during the growing season appears stronger than that for increased resource access through removal of obstructing grass structures during the dormant season. Facilitation may benefit the nutritional gains obtained by certain species in the short term, but these benefits do not appear to be translated into the expected population consequences. In collaboration with co-author Norman Owen-Smith, we

suggested this could be due to seasonal tradeoffs between facilitation and competition, as well as to restrictions on the spatial extent of trophic overlap.

In Chapter 3 we compared the grass height use in relation to body size. We expected that the grass height favoured would increase with the body size of the herbivore species, as suggested from past studies of resource partitioning among large mammalian herbivores. Instead we found that the largest of these species, white rhino, concentrated on the shortest grass, while the smallest species, impala, favoured grass heights intermediate between those grazed by wildebeest and zebra. Results suggest that the scaling of mouth width relative to body size, and hence metabolic demands, is the primary factor governing grass height selection, rather than body size alone. Hence grazing successions governed by body size differences may not be a typical feature of their ecology, contrary to past suggestions. Furthermore, there was considerable overlap in grass height grazed among these four species, indicating that niche separation by grass height is inadequate alone to explain their coexistence. More attention needs to be paid to other aspects such as the grass species selected and habitat structure favoured.

Chapter Four compared the overlap in grassland and grass species use, as well as grass height and grass greenness of swards grazed by the herbivores over the dry season. I show that all species prefer grazing lawns during times of abundance. Zebra leave grazing lawns before other species, and wildebeest leave grazing lawns before white rhino and impala. This suggests zebra and wildebeest may be competitively excluded from grazing lawns through a reduction in grass height, by white rhino and impala, during the dry season. A high dry season overlap was also found between the herbivores in Themeda, woodland and other grasslands, such that species do not appear to be partitioning these resources based on feeding patch or grass species. The unique aspect of this research is the presence of the megaherbivore, white rhino. White rhino are potentially the ‘supreme’ facilitator increasing the availability of nutritious grazing lawns, as well as increasing the quality of those lawns through grazing in the wet season. However, white rhino can out compete other herbivores by reducing grass quantity on those lawns. Future research is needed to better understand the trade-off between facilitation and competition by megaherbivores.

The major limitation of this research is that I am unable to relate feeding impacts in the short term, to population impacts in the long term. This is a common problem with large mammal studies. For example, it is difficult and time consuming to measure changes in large herbivore populations, and large scale experiments such as fenced exclosures and animal removals are prohibitive. Modelling is one way to better understand whether nutritional gains or losses in the short term lead to population consequences. Norman Owen-Smith is currently developing a model and manuscript addressing some of these ideas. We intend to collaborate and incorporate data from this research.

This is the first study to my knowledge to show in detail that competitive exclusion for short swards is a potential mechanism of competition. Future research needs to address how populations are affected by such mechanisms before we can make conclusions about the importance of interspecific competition on co-existence of large herbivores. I did not find evidence in my study for the mechanism, where some species exclude others by reducing the quality of swards. However, visual estimates of grass greenness may be unable to detect such quality differences in swards. The impact of this mechanism would likely be greatest in medium to tall grass swards in the early dry season. Evidence is still needed that some species avoid mutually preferred swards during the early dry season due to reduced quality. An interesting point is that both mechanism, i.e. competition for grazing lawns and competition for higher quality medium to tall swards, would mainly occur during the same period, the early dry season. Therefore the early dry season may be the important period for competition between herbivores, as oppose to the late dry season.

But once again, without relating the short term feeding impacts to long term population impacts, the importance of interspecific competition in governing populations is uncertain. I personally doubt that exploitative competition is a major force regulating populations and coexistence. Yes, theoretically interspecific competition will occur at high enough densities. But densities in the natural world are likely lower than that threshold. For example, the density or biomass of cattle on grazing lands far exceeds any densities or biomass seen in natural places. Also I must reiterate that no studies to date have convincingly demonstrated that competition and facilitation is governing populations.

Although there has been much debate about the conclusions of Hairston, et al. (1960), I tend to agree that herbivores may not be governed by competition. I agree that other factors such as predation and disease may better explain population changes, than interspecific competition. Interspecific competition may be occurring within localized spatial scales, but not to the extent where it is a major governing force.

I also believe that the guild of grazers we observe today are all in some way generalists, which also reduces the potential for competition leading to population impacts. Most herbivores observed graze the best grass on offer, and then the second best grass on offer. They may have different body sizes and mouth sizes, but all of these differences may have been adapted due to the pressure to be generalists. For example, impala are grazer/browsers and can eat grass at various heights. White rhino can graze very short grasslands and digest very fibrous grass as well. Zebra are thought to generalists and wildebeest sit somewhere in between. Research into the evolutionary record of herbivores may show that overly specialist herbivores have gone extinct compared to more generalist herbivores. It would seem that fluctuations in rainfall and spatial and temporal heterogeneity would be best dealt with by generalist feeding strategies.

Finally, if interspecific exploitative competition does not govern populations, it likely does not lead to evolutionary adaptations and change. For example, how does a zebra know, that a wildebeest grazed the grass the day before? Other than herbivores that can alter habitats, I do not believe that grazing species can change the structure of grass in a specific way, such that there is a mechanism for another species to adapt a different strategy in evolutionary time. I guess I see the world of grazing herbivores as being more similar than more different. I have shown in this study the large overlap in grass grazing. I believe there is an inherent problem with observational based studies, that if you look for differences, you will always find them. Do herbivores partition resources to minimize competition or due to the 'ghost of competition"? Probably not. For herbivores, it's a "first come first served" world of food, where you can also be eaten yourself.

References

Hairston, N., Smith, F.E. and Slobodkin, L. (1960). Community structure, population control, and competition. American.Naturalist 94:421-5.